PATTERNS OF HABITAT USE AND SEGREGATION AMONG AFRICAN LARGE CARNIVORES

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PATTERNS OF HABITAT USE AND SEGREGATION AMONG AFRICAN LARGE CARNIVORES

A CASE STUDY ON THE AFRICAN WILD DOG (*LYCAON PICTUS*), THE SPOTTED HYENA (*CROCUTA CROCUTA*) AND THE LION (*PANTHERA LEO*)

Gabriele Cozzi

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This thesis is dedicated to the memory of

Christine B. Müller

a mentor, a colleague, a friend

CONTENTS

SUMMARY

This work investigated patterns of habitat use and segregation among species of the large African carnivore guild: the African wild dog, the spotted hyena and the lion. In particular, I studied what role temporal and spatial partitioning of activities, respectively, use of space may play in promoting coexistence. The study site was the Okavango Delta in northern Botswana, one of the few remaining places in Africa where the three species still co-occur in a pristine and undisturbed ecosystem.

In *Chapter Two* we investigated the degree of temporal segregation between the allegedly diurnal wild dogs and the nocturnal spotted hyenas and lions. Wild dogs are commonly described as day active, and such behaviour has been described as an adaptation to evade interactions with the two other dominant species. We, however, showed a degree of temporal overlap considerably higher than previously described. Such overlap was mainly due to the unexpected nocturnal behaviour of wild dogs that was mainly influenced by moonlight availability, rather than by the activity of hyenas and lions. Our results thus raise some questions concerning the real role of spotted hyenas and lions in shaping the activity patterns of wild dogs and highlight how temporal overlap may only play a marginal role in enhancing coexistence among the species.

Chapter Three demonstrated that the spatial distribution of wild dogs was negatively influenced by the distribution of lions, but not by that of spotted hyenas. In areas catheterized by a low lion presence, wild dogs may take advantage of the best resources, but they were restricted in their behaviour or even excluded from particular areas above a certain lion density, and this irrespectively of other variables such as habitat type and prey availability. Our results highlighted spatial segregation as a key mechanism promoting coexistence between wild dogs and lions. Considering the dramatic rate at

which habitat loss and fragmentation are happening, the need for space that allows species coexistence should sound like a warning bell.

In *Chapter Four* we investigated how the species are affected by and adapt to anthropogenic habitat modification and human activities near the boundary of a protected area. Specifically, we analysed how different types of barrier influenced the distribution and spatial interaction among species and discussed their effects at the community composition level. We showed that lions were restricted in their movements by an artificial fence erected to control the movement of ungulate species, while the other carnivore species freely crossed it. In contrast, lions were not obstructed in their movements by rivers, which represented an almost completely impassable barrier for the smaller spotted hyenas and wild dogs. Reinforcing the findings of *Chapter Three*, *Chapter Four* provided further evidence that wild dogs may take advantage of areas characterized by a low lion presence, particularly for critical activities such as raising offspring.

Chapter Five presents density estimates for spotted hyenas and lions in the study area. An accurate estimate was necessary because the intensity of interaction between competing species partly depends on the density at which each species occurs. We calculated a density of 15.4 adult hyenas /100 km^2 and 16.2 lions /100 km^2. These figures compared well with other highly productive ecosystems of southern and eastern Africa. The hyena and lion density in the Okavango Delta should therefore be considered to be between medium and high.

ZUSAMMENFASSUNG

Die vorliegende Dissertation untersuchte Raumnutzung und Segregation zwischen verschiedenen Arten der Gilde afrikanischer Großraubtiere: der Afrikanische Wildhund, die Tüpfelhyäne und der Löwe. Insbesondere studierte ich, wie die zeitliche und räumliche Aufteilung der Aktivitäten, beziehungsweise der Habitatsnutzung, das Zusammenleben der Tiere beeinflusst und fördert. Das Untersuchungsgebiet war das Okavango Delta im Norden Botswanas, einer der wenigen verbliebenen Orte in Afrika, wo die drei Arten in einem unberührten und ungestörten Ökosystem vorkommen.

In *Kapitel Zwei* untersuchten wir die zeitliche Trennung zwischen den angeblich tagaktiven Wildhunde und den nachtaktiven Tüpfelhyänen und Löwen. Wildhunde werden allgemein als tagaktiv beschrieben, und dieses Verhalten ist als Anpassung beschrieben worden, um Wechselwirkungen mit den anderen beiden dominanten Arten zu reduzieren. Wir konnten jedoch eine wesentlich höhere zeitliche Überlappung zwischen den drei Arten aufzeigen als zuvor beschrieben worden war. Diese Überlappung war vor allem durch das unerwartete, nächtliche Verhalten der Wildhunde bedingt. Ihre Nachtaktivität war durch die Mondlichtverfügbarkeit, jedoch nicht durch die Aktivität von Hyänen und Löwen, beeinflusst. Unsere Ergebnisse werfen somit einige Fragen über die eigentliche Rolle der Tüpfelhyänen und Löwen bei der Gestaltung der Aktivitätsmuster der Wildhunde auf. Ausserdem zeigen unsere Resultate, dass zeitliche Überlappung nur eine marginale Rolle bei der Verbesserung der Koexistenz zwischen den Arten spielen darf.

Kapitel Drei zeigte, dass die räumliche Verteilung von Wildhunden durch die räumliche Verteilung von Löwen negativ beeinflusst wird, aber nicht durch jene von Tüpfelhyänen. In jenen Gebieten, welche durch eine niedrige Löwenpräsenz charakterisiert sind, können Wildhunde von den besten Ressourcen profitieren. Ab einer bestimmten Löwendichte sind sie aber in ihrem Verhalten eingeschränkt oder gar aus bestimmten

Bereichen ausgeschlossen – und dies unabhängig von anderen Variablen wie Vegetationstyp oder Beuteverfügbarkeit und -verteilung. Unsere Ergebnisse weisen darauf hin, dass räumliche Segregation ein wichtiges Element zur Förderung der Koexistenz zwischen Wildhunde und Löwen ist. Angesichts der dramatischen Geschwindigkeit, mit welcher Lebensraumverlust und -fragmentierung vorwärtsschreiten, sollte uns der Raumbedarf, welcher für das Zusammenleben von Arten notwendig ist, alarmieren.

In *Kapitel Vier* untersuchten wir, wie sich Wildhunde, Tüpfelhyänen und Löwen an anthropogenen Landschaftsveränderungen und menschlichen Aktivitäten in der unmittelbaren Nähe eines Schutzgebietes anpassen. Konkret untersuchten wir, wie verschiedene Typen von Barrieren die Verteilung und räumliche Interaktion zwischen den Arten beeinflussen. Wir zeigten, dass Löwen durch einen künstlichen Zaun, welcher für Huftieren gebaut worden war, in ihren Bewegungen beschränkt waren, während die anderen zwei Raubtierarten den Zaun regelmässig überquerten. Im Gegensatz dazu waren Löwen in ihren Bewegungen durch Flüsse nicht beeinflusst; dieselben Flüsse stellten aber eine fast unüberwindliche Barriere für die kleineren Tüpfelhyänen und Wildhunde dar. *Kapitel Vier* liefert einen weiteren Beweis, dass Wildhunde von Gebieten, welche durch eine niedrige Löwenpräsenz charakterisiert sind, profitieren können – dies insbesondere für kritische Aktivitäten wie die Aufzucht der Nachkommen. Dieses Kapitel stärkt somit die Ergebnisse von *Kapitel Drei*.

Kapitel Fünf präsentiert Dichtschätzungen für Tüpfelhyänen und Löwen. Weil die Intensität der Wechselwirkung zwischen konkurrierenden Arten teilweise von der Dichte abhängt, war eine genaue Schätzung notwendig. Wir berechneten eine Dichte von 15.4 erwachsene Hyänen/100 km^2 und 16.2 Löwen/100 km^2. Diese Zahlen stimmen mit denjenigen von anderen hochproduktiven Ökosystemen im südlichen und östlichen Afrika überein. Die Hyänen und Löwen im Okavango Delta weisen daher eine mittlere bis hohe Dichte auf.

Chapter One

General Introduction

The aim of this introduction is to put my research in a general context, to briefly describe the study system, the study area and the general methods used, and to outline the structure of the thesis. More detailed information is presented, where pertinent, in each individual chapter.

CARNIVORES ON THE BRINK OF EXTINCTION

Guilds of large carnivores, once widespread on all five continents, have experienced a dramatic decline during the late Pleistocene and the modern era (Barnosky et al. 2004, Koch and Barnosky 2006, Turvey and Fritz 2011). For example, until around 12,000 years ago, a guild of carnivores including the saber-toothed cat *Smilodon populator* and the bulldog bear *Arctodus simus* occupied North America (Carrasco et al. 2009), while, in the last 100 years, the Asian guild has almost lost both the cheetah *Acinonyx jubatus venaticus* and the lion *Panthera leo persica* (Sinha 2002). The African guild, which has suffered no extinctions during the last million years, thus represents the last intact guild of large carnivore species (Valkenburgh 1988, Dalerum et al. 2009).

Seven species belong to the guild: the African wild dog *Lycaon pictus*, the cheetah *Acinonyx jubatus*, the leopard *Panthera pardus*, the striped hyena *Hyaena hyaena*, the brown hyena *H. brunnea*, the spotted hyena *Crocuta crocuta*, and the lion *P. leo*. With exception of the two *Hyaena* species that are predominantly scavengers, all other species are characterized by a pronounced predatory behavior and are commonly referred to as members of the African large predator guild (Hayward and Slotow 2009). Even this last intact guild of large predators is, however, facing extinction. African wild dogs have disappeared from 25 of the 39 countries in which they were found historically, and the overall population is estimated at about 5,000 free-ranging individuals (Woodroffe et al. 1997). Cheetahs have faced a similar fate, and large and contiguous populations can be found mainly in Eastern (e.g. Kenya and Tanzania) and Southern Africa (e.g. Namibia and

Botswana). Less than 15,000 cheetahs survive in the wild (Freeman et al. 2001). The numbers of spotted hyenas and lions are equally declining throughout their distribution ranges. Despite being fairly broadly distributed across the African continent, spotted hyenas are second only to the highly endangered Ethiopian wolf *Canis simensis* and the African wild dog in the list of the species whose conservation needs to be prioritized (Gittleman et al. 2001). Lion numbers declined drastically during the second half of the 20th century and a recent survey estimates a maximum of 30,000 free-ranging individuals continent-wide (Bauer and Merwe 2004). Today, healthy and stable populations of large carnivores mainly persist in large protected areas (Gittleman et al. 2001). One such protected area is the Okavango Delta in northern Botswana, a 20,000 km^2 pristine ecosystem where all species of the large African predator guild still co-occur and where my study took place (Fig. 1).

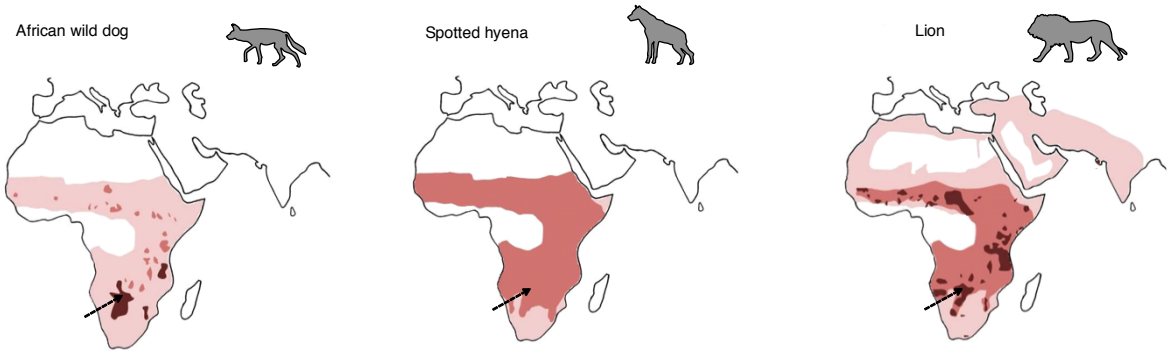

Figure 1: *Historical (○), present (●) and strongholds (●) for African wild dogs, spotted hyenas and lions. The black arrows show the study area in the Okavango Delta ecosystem, one of the few places where all species of the large African predator guild still co-occur (Adapted from: Macdonald 2001).*

INTRAGUILD INTERACTIONS – PREDATION AND COMPETITION

The causes for the decline of large predator species, which has dramatically accelerated in last 50 years, are manifold and comprise direct persecution by humans resulting from

human-wildlife conflicts, the fragmentation and loss of habitats to agriculture and other human activities, a reduced prey base, the spreading and introduction of diseases through human activities, and an increasing demand for animals and animal parts by the black market (Woodroffe and Ginsberg 1998, Woodroffe 2000, Daszak et al. 2001, Carbone and Gittleman 2002, Treves and Karanth 2003, Gratwicke et al. 2008, Alexander and McNutt 2010, Woodroffe and Donnelly 2011). Due to human-induced habitat loss, species are forced within smaller areas. Consequently, interspecific interactions among guild members are likely to increase in the future.

Because a guild is defined as a functional (rather than taxonomical or phylogenetical) group of organisms in a community that share the same or similar resources, guild members show similar behavioural, morphological and physiological adaptations and characteristics (Simberloff and Dayan 1991). It can thus be anticipated that interactions (e.g. competition) among guild members may be particularly pronounced. Segregation in some of the most important dimensions of the ecological niche – notably food, space and time – is thus a fundamental requirement for the co-existence of competing guild members (Vandermeer 1972, Schoener 1974a, Levine 1976, Linnell and Strand 2000).

Guild members, in both extinct and extant guilds, are characterized by a considerable variation in body size, which suggests strong interspecific dominance hierarchies resulting in the larger members of the guild dominating the smaller members (Maynard-Smith and Parker 1976, Polis and Holt 1992, Palomares and Caro 1999, Woodward and Hildrew 2002). Interspecific interactions among guild members manifest in the form of intraguild predation and intraguild competition. Intraguild predation acts unidirectional with the larger and stronger guild members killing the smaller members. Intraguild competition may instead act either unidirectional in the case of direct competition, for instance in the form of kleptoparasitism, or bidirectional in the form of

indirect or exploitation competition (Levine 1976). Overall, subdominant species are therefore likely to suffer the most from habitat 'crowding' and the resulting increase of negative interspecific interactions within smaller spaces (Polis and Myers 1989, Holt and Polis 1997, Durant 2000).

Much emphasis has been placed on the effects of predator species on prey populations, but far less attention has been paid to the effect that predators have on each other (Linnell and Strand 2000). Yet, the interplay of intraguild predation and intraguild competition can greatly influence species co-existence or exclusion, and thus community composition. Only relatively recently have intraguild predation and competition gained increasing attention, and are now recognized as an important ecological factor influencing population dynamics of carnivores (Palomares and Caro 1999, Caro and Stoner 2003). Worldwide, predation by and competition with dominant members of the carnivore guild may be partially responsible for the rarity of competitively inferior carnivore species inhabiting the same ecosystem as more dominant ones (Palomares and Caro 1999, Caro and Stoner 2003), and for slow recovery following population declines (Vucetich and Creel 1999). Understanding the ecological factors that regulate intraguild interactions (i.e. intraguild predation and competition), and the consequences that such interactions have on population dynamics, has important conservation implications, especially since competitively inferior species are often the most endangered.

Despite the asymmetric dominance hierarchies among species of the same guild and the negative effects of intraguild predation and intraguild competition, subdominant species can coexist with their dominant counterparts through partitioning of habitats and resources (Pianka 1974, Schoener 1974a, Levine 1976, Durant 1998, Linnell and Strand 2000, Holt and Barfield 2003, Harrington et al. 2009, Levine and HilleRisLambers 2009). Environmental heterogeneity, for instance, can lead to co-existence of interacting species by providing refuges from strongly negative interactions (predation and competition) in

space and time. Competitively inferior species may occupy suboptimal habitat types to evade interactions with stronger species (Chesson and Warner 1981, Chesson 1986, Durant 1998). However, refuge availability and effectiveness change through time according to changes of habitat use and activity by the interfering species on a daily and seasonal basis. Patterns of habitat use and activity by the competitively stronger species are likely to influence the habitat use of the less competitive species. In the past the spatial distribution of carnivore species has been associated with prey availability (Macdonald 1983), but more recently intraguild interfering species have been shown to negatively influence each other's distribution.

Nevertheless, the plasticity of animal species to adapt to ecological settings is limited by their evolutionary adaptations (Schoener 1974b). For example, (Kronfeld-Schor and Dayan 2003) suggested that temporal behavioural responses (e.g. to predation or competition) are more commonly manifested in a restriction of activity within the active part of the diel activity cycle, rather than in a complete shift of activity times. Predators searching for the same prey will inevitably do so at times where the prey is most vulnerable, and hunting most favourable. Their rate of encounter may thus be high and strongly influenced by the activity patterns and the habitat preferences of their common prey species. This may be particularly true for the members of the large African carnivore guild that heavily rely upon the same prey base (Mills and Biggs 1993, Hayward and Kerley 2005, Hayward et al. 2006a, Hayward 2006, Hayward et al. 2006b, Hayward et al. 2006c).

STUDY SYSTEM

African wild dogs are medium-sized predators that live in highly cohesive groups (packs) averaging 8–12 adults and their associated offspring (McNutt 1995, Creel and Creel 2002) (Fig. 2). They need and range over comparatively large territories, and habitat loss and

fragmentation may thus have contributed to the decline of the species (Woodroffe et al. 1997) (Fig. 1). Even within large protected areas, however, wild dogs occur at very low densities and evidence suggests that they have never been numerous (Selous 1908, Schaller 1972, Malcom 1979, Mills and Biggs 1993). Where they co-occur with other large carnivore species, their density may be one to two orders of magnitude lower than the density of spotted hyenas and lions (Creel and Creel 1996). Due to their small body size (25–30 kg), wild dogs are competitively inferior to the larger and equally social spotted hyenas (50–80 kg) and lions (120–240 kg), who have thus been proposed to be partly responsible for the low density at which wild dogs occur (Creel and Creel 1996, McNutt and Boggs 1996, Mills and Gorman 1997, Gorman et al. 1998, Creel 2001, Carbone et al. 2005).

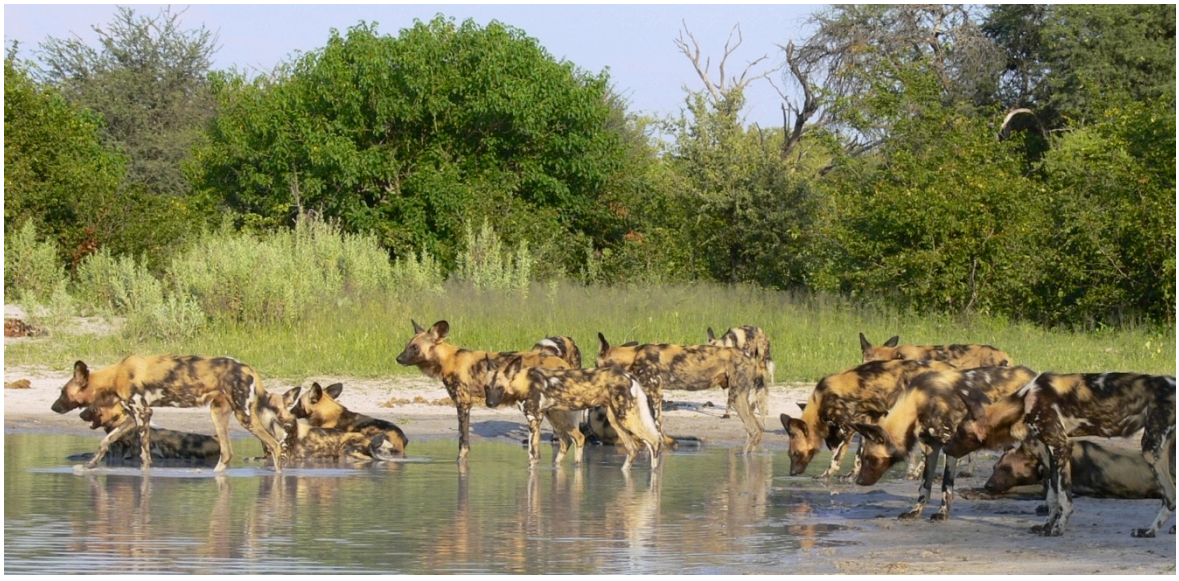

Figure 2*: A pack of wild dogs in the Okavango Delta in northern Botswana. The Delta, a 20,000 km^2 pristine ecosystem, is home to a population of wild dogs estimated at a few hundred individuals, representing the largest contiguous population of wild dogs on the continent.*

Spotted hyenas mainly influence wild dogs negatively by kleptoparasitizing (stealing) their kills. In the open plains of Eastern Africa, where visibility is not obstructed by vegetation, spotted hyenas were recorded at 85% of wild dog kills (Fanshawe and Fitzgibbon 1993). In contrast, in more densely vegetated areas, where locating and aggregating to a kill is more difficult, hyenas only rarely appropriated kills from wild dogs (Creel and Creel 1996). Nevertheless, hyena presence may negatively influence wild dogs by reducing their feeding success and feeding time with negative consequences on their reproductive success (Fuller and Kat 1990, Carbone et al. 1997, Carbone et al. 2005).

Gorman et al. (1998) further suggested that, because of the high energetic costs of hunting, loss of kills to spotted hyenas might explain why the density of wild dogs is low in those regions where the risk of kleptoparasitism is high. Although large packs of wild dogs can repel single hyenas or hyenas travelling in small groups of 2–3 individuals, the relationship between the two species is heavily biased to the benefit of the latter (Fig. 3). However, only a few cases of hyenas killing wild dogs have been reported and these were mainly young individuals (e.g. pups unattended at den sites), or injured individuals separated from the rest of the pack (Woodroffe et al. 1997, J.W. McNutt, pers. comm.). Nevertheless, serious injuries resulting from hyena bites during a fight may eventually end up with tragic consequences for a wild dog.

Lions kleptoparasitize wild dog kills considerably less than spotted hyenas do (pers. obs.) and mainly influence wild dogs negatively through direct predation. Across different ecosystems, lions represent the major cause of natural mortality among adult and young wild dogs, accounting for up to 80% of the cases of predation by large carnivores (Woodroffe et al. 1997). Predation by lions has, for example, been considered one of the causes of the failed reintroduction of wild dogs into Etosha National Park, Namibia (Scheepers and Venzke 1995). On a large spatial scale, wild dogs have been shown to avoid areas with high lion densities (Mills and Gorman 1997, Creel and Creel 2002), and

this has been proposed as an additional element supporting the negative effect of lions on wild dog populations (Fig. 4).

Figure 3*: A pack of wild dogs mobbing a spotted hyena in the Okavango Delta in northern Botswana. Working synergistically in a group, wild dogs successfully defend their kills from single spotted hyenas, while they succumb when several hyenas aggregate at kill sites.*

STUDY AREA

From a scientific as well as a conservation perspective, the Okavango Delta in northern Botswana (Fig. 5) represents a unique opportunity to investigate patterns of spatial and temporal partitioning among large carnivore species and the mechanisms leading to their coexistence, for several reasons: (1) African wild dogs, spotted hyenas and lions co-occur in the delta, and the ecosystem associated with the Okavango River has been little modified by human footprint. (2) Wild dogs are on the verge of extinction, and predation by and competition with spotted hyenas and lions have been proposed to be among the major natural causes for this and for the low natural density at which wild dogs occur. (3) The Okavango ecosystem hosts one of the largest, continuous natural populations of

Figure 4: *A male lion in the Okavango Delta in northern Botswana. Lions are the largest and heaviest of the African carnivore species and do not suffer direct competition by the other members of the guild.*

African wild dogs in the world and thus plays a key role in the conservation of the species. (4) The delta consists of a heterogeneous landscape of small scale, different habitat types ranging from perennial floodplains, to grasslands, mixed *Acacia* spp. sandveld and mopane *Colophospermum mopane* woodlands, providing an ideal study system to investigate patterns of habitat use and spatial partitioning.

The landscape is characterized by the flooding regime of the Okavango River that, after a 1,600 km long path that starts in the highlands of southeast Angola, disappears into the sand of the Kalahari Desert, forming Africa's largest inland alluvial fan (Mendelsohn et al. 2010). The extent of flooding depends on rainfall in the catchment area in Angola as well as on the local seasonal cumulative precipitation (November – March); during wet years the delta swells to three time its permanent size. The flood takes several months to reach the distal terminus of the delta, and flood levels in the study area typically peak in

July and subside rapidly during the dry summer months. The lowest water level is reached early in the calendar year when increasing local rains have sufficiently recharged the region's groundwater table. Water is available all year round and, apart from zebras *Equus burchellii antiquorum* and to a lower extent buffalos *Syncerus caffer*, the herbivore species that constitute the bulk of the diet of wild dogs, spotted hyenas and lions are relatively sedentary (Bartlam 2010, Bennit 2012).

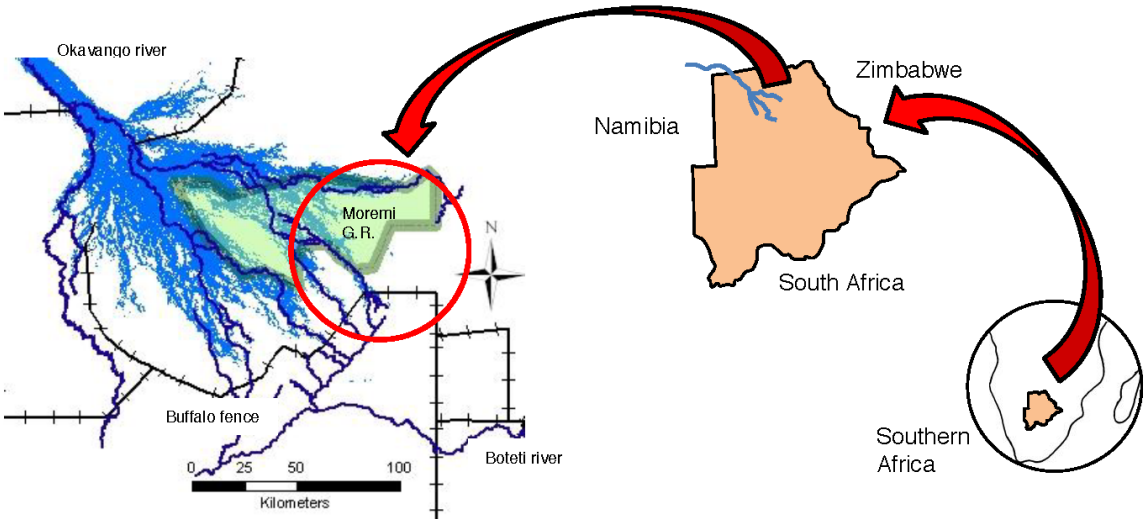

Figure 5: *The study area in the Okavango Delta, Northern Botswana (red circle) comprising the South-Eastern section of the Moremi Game Reserve and the adjacent Wildlife Management Areas. Several branches break away from the Okavango River and, together with their associated floodplains, form Africa's largest inland delta. A veterinary cattle fence (buffalo fence) erected to separate buffalos and cattle and avoid the transmission of the foot-and-mouth disease represents the southern boundary of the study area and is the most prominent human-made feature in the ecosystem.*

GENERAL METHODS

To simultaneously collect information about spatial distribution and activity patterns for animals that range over thousands of kilometres, several individuals in multiple social units were fitted with radio-collars (Vectronic Aerospace GmbH, Germany) equipped with a

VHF (very high frequency) beacon sender, a GPS (global positioning system) device and two bidirectional motion sensors. The collars were scheduled to record several GPS locations each day and to continuously record activity data that were summed over 5-minute intervals. Collar size and weight depended on the species: wild dogs were fitted with collars weighing less than 300 g (≈ 1 % of the species body weight) and spotted hyenas and lions with collars weighing about 700 g (<1 % of the species body weight). A Botswana registered veterinarian was responsible for the anaesthesia during the collaring procedure. Drugs composition and quantity used to tranquillize the animals varied according to the species and the situation and followed standard protocols. Wild dogs were anesthetized with a mixture of ketamine and xylazine, reversed with yohimbine (for further details see: Osofsky et al. 1996); spotted hyenas with a mixture of ketamine, telazol (a compound product of tiletamine and zolazepam) and medetomidine, reversed with antisedan, and lions with a mixture of telazol and medetomidine, reversed with antisedan (for further details see: Kock et al. 2006). The drugs were injected through a dart shot from a CO_2-pressurized dart-gun (Dan-Inject, Denmark) at distances ranging from 15 to 35 m. During the anaesthesia the general health of each sedated animal was recorded, body measurements were taken and blood samples collected. Finally a radio-collar was attached to the animal and the anaesthesia reversed (Fig. 6). After collaring, animals were checked at regular intervals to ensure that the collar did not represent a physical impediment and did not negatively affect them.

On a typical day, one or more collared animals were located from the ground while tracking for the VHF beacon emitted by the collars (each collar emitted a VHF beacon with a unique frequency) that typically ranged between 1 and 2 km. At each sighting, information such as time, GPS coordinates, vegetation type, group composition, reproductive stage (e.g. pregnancy), physical conditions and activity were recorded. Animals were mainly located early morning and late afternoon when the chance of

observing activities such as hunting was higher than during the hot midday hours. On occasion, and depending on the vegetation type, animals were followed throughout the night. When an animal was found at a carcass, prey species, gender, age and days since the kill was made were also noted. If an animal could not be located from the ground (e.g. because it moved to a remote area with a limited road network) for more than two weeks, aerial VHF tracking was done from a Cessna 182 plane, the location of the animal was roughly pinpointed, and the animal was subsequently visited on the ground.

Figure 6: *Study animals were fitted with GPS radio-collars which recorded several locations per day to accurately monitor their use of the territory. During the anaesthesia the animals were blindfolded to reduce stressful stimuli (visual and auditory) and body measures and blood samples taken. Wild dogs were anesthetized during the day while, in the majority of the occasions, darting of spotted hyenas and lions occurred at night.*

CONCEPT AND OUTLINE OF THE THESIS

Interestingly, despite the apparent large effect of lions and spotted hyenas upon wild dog, only few attempts have been made to quantify their impact on the population dynamics of wild dogs. The topic seems to have reached its apex towards the end of the 1990s, culminating with a series of published works (Ginsberg et al. 1995, Scheepers and Venzke 1995, Creel and Creel 1996, Carbone et al. 1997, Mills and Gorman 1997, Creel and Creel 1998, Gorman et al. 1998, Vucetich and Creel 1999, Creel 2001). However, the majority of

these published studies are purely qualitative. But what are the real effects of lions and spotted hyenas on the population dynamics and the survival of the endangered African wild dog? How do co-occurring wild dogs, spotted hyenas and lions affect each other's behaviour and ecology, and what are the mechanisms leading to their co-existence? Is inhibition by lions and spotted hyenas the cause for the low density at which wild dogs occur in those large protected habitat where conditions seem to be optimal for large carnivores?

The aim of my thesis is not to find an ultimate answer to all of those ambitious questions (pretending to answer questions that have puzzled scientists for decades would appear arrogant and presumptuous), but rather to collate and present quantitative scientific data that deepen our understanding of the relationships among co-occurring large predators and the mechanisms leading to their coexistence. The future of African large carnivores is likely tightly coupled with their survival within protected areas that increasingly need to be managed. Understanding how these species interact with each other and ultimately coexist is crucial if we want to maintain ecosystem functioning and avoid being able to observe an African wild dog only next to a *Smilodon*; in a museum.

Within the general framework of interactions and co-existence between guild members, I focus on (1) patterns of activity and temporal partitioning among African wild dogs, spotted hyenas and lions, and (2) their patterns of habitat use and avoidance on a within-territory fine spatial scale. Testing for the influence of one species on another would involve removing one species and looking for a change in the behaviour of the other species; such an approach is clearly impractical and not desirable for endangered species living within protected areas. Instead, my study combines direct field observation and data continuously recorded by radio-collars fitted on several individuals of each species.

Because cheetahs, similarly to wild dogs, suffer predation by and competition with spotted hyenas and lions (Durant 2000), I included pertinent data on cheetahs in the

analysis to broaden and strengthen the breadth of the results and conclusions. This was done in collaboration with Femke Broekhuis, a PhD student at the Wildlife Conservation Research Unit (WildCRU) at the University of Oxford also working in the Okavango Delta, who is consequently co-author on my manuscripts. Furthermore, Mrs. Broekhuis and I worked synergistically in gathering general information about the study area such as the characterisation of habitat types, distribution and abundance of prey species through herbivore censuses, and these data are equally shared and part of our respective Theses and manuscripts.

All the chapters of my thesis are organized as self-contained manuscripts that have been or will be submitted to peer-reviewed journals. This inevitably results in some overlap among them, and particularly in the study site section of each manuscript. Specifically, my thesis contains the following chapters:

Chapter Two challenges the general belief that the previously described diurnal and crepuscular activity pattern of African wild dogs and cheetahs is a behavioural adaptation to avoid encounters with the predominantly night-active spotted hyenas and lions. Combining high-resolution activity data collected on several individuals of the four species, I was able to show an extensive temporal overlap between the members of the guild that was mainly due to a previously undescribed nocturnal activity of wild dogs and cheetahs.

Chapters Three and Chapter Four contain detailed spatial observational data necessary to investigate patterns of habitat use and segregation among the three co-occurring species. In chapter 3, I combine geographic information system (GIS) data on habitat characteristics with GPS location data from five packs of wild dogs to determine preferred habitat types. I then focus on one pack, whose territory completely overlaps with the territories of several groups of spotted hyenas and lions, to investigate patterns of within-territory avoidance. On a broad spatial scale, the density of wild dogs have been

shown to negatively correlate with the density of lions and spotted hyenas but little is known about patterns of avoidance at a finer, within-territory spatial scale. In chapter 4, I investigate how the species are affected by and adapt to a human-related modification of the landscape. Specifically, I compare the effects of an artificial and a natural barrier on the habitat use and ranging behaviour of the four species (cheetahs are included in this study too) and analyse the consequences that differential barrier permeability have on the spatial distribution and spatial relationships among the species.

Chapter Five contains density estimates for the subpopulations of spotted hyenas and lions living within the study area. In this chapter I explain how animals are attracted by means of playback sounds, and density estimates are then obtained from the number of individuals arriving at multiple calling stations. I furthermore investigated methodological variables on distributions and densities that might influence results, including habitat type, seasonality, and responses to varying broadcast call types. The density of wild dogs is, however, well known from previous studies. Accurately estimating the number of individuals is necessary because the intensity of interaction between competing species partly depends on the density at which each species occur. This furthermore allows comparing the intensity of interaction in the study area (see for example chapter 2 and 3) with findings from other sites.

In *Chapter Six* I synthesize the results from the previous chapters and discuss the findings of my work in a broader, conservation-oriented context. Populations of large carnivores are declining worldwide and a deeper understanding of the factors regulating their coexistence is necessary to conserve species diversity and ensure the functioning of ecosystems.

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Chapter Two

Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology* (2012)

Top: A pack of wild dogs getting ready for the daily hunt at dusk. On moonlight nights, wild dogs extend their activity well into the night despite the costs associated with the risk of encountering the night active hyenas and lions.

Bottom: When night falls hyenas often gather together (here at the communal den) to socialize or set off to hunt. Like lions, hyenas are predominantly nocturnal and represent a serious risk to wild dogs and cheetahs.

Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores

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Running Headline: Patterns of activity in large carnivores

ABSTRACT

Africa is home to the last intact guild of large carnivores, and thus provides the only opportunity to investigate mechanisms of coexistence among large predator species. Strong asymmetric dominance hierarchies typically characterize guilds of large carnivores; but, despite this asymmetry, sub-dominant species may persist alongside their stronger counterparts through temporal partitioning of habitat and resources. In the African guild, the sub-dominant African wild dogs and cheetahs are routinely described as diurnal and crepuscular. These activity patterns have been interpreted to result from the need to avoid encounters with the stronger, nocturnal spotted hyenas and lions. However, the idea that diel activity patterns of carnivore species are strongly shaped by competition and predation has recently been challenged by new observations. In a three-year study in the Okavango Delta, we investigated daily activity patterns and temporal partitioning for wild dogs, cheetahs, spotted hyenas and lions by fitting radio-collars that continuously recorded activity bursts, to a total of 25 individuals. Analysis of activity patterns throughout the 24-hour cycle revealed an unexpectedly high degree of temporal overlap among the four species. This was mainly due to the extensive and previously undescribed nocturnal activity of wild dogs and cheetahs. Their nocturnal activity fluctuated with the lunar cycle, represented up to 40% of the diel activity budget and was primarily constrained by moonlight availability. In contrast, the nocturnal activity patterns of lions and hyenas were unaffected by moonlight and remained constant over the lunar cycle. Our results suggest that other ecological factors such as optimal hunting conditions have shaped the diel activity patterns of sub-dominant, large predators. We suggest that they are 'starvation driven' and must exploit every opportunity to obtain a meal. The benefits of activity on moonlit nights therefore offset the risks of encountering night-active predators and competitors.

Key-words: Coexistence; temporal niche; predator–predator relationships; costs-benefits; activity data-loggers; nocturnal activity; moonlight; African carnivore guild.

INTRODUCTION

Intraguild competition and predation have been recognized as important ecological factors influencing the population dynamics of carnivores (Palomares and Caro 1999, Linnel and Strand 2000, Caro and Stoner 2003). For example, interactions with dominant species could be responsible for the general rarity of competitively inferior predator species (Palomares and Caro 1999, Caro and Stoner 2003) and may push some species, such as the African wild dog (*Lycaon pictus*), to the edge of extinction (Vucetich and Creel 1999). Understanding the relationships among the members of a guild is particularly important for large carnivores as they tend to be extinction-prone, due to low population densities and low reproductive rates (Purvis et al. 2000). Furthermore, human-induced habitat loss and fragmentation are forcing carnivores to inhabit ever-smaller areas, increasing the frequency of antagonistic interactions and hence potentially accelerating extinction rates (Creel 2001, Caro and Stoner 2003).

Prior to a wave of extinctions during the Late Pleistocene and the modern era, guilds of large predators were widespread on all five continents (Barnosky et al. 2004, Koch and Barnosky 2006, Turvey and Fritz 2011). Today, however, an intact guild of large predator species can be found only in Africa (Valkenburgh 1988, Dalerum et al. 2009). The African guild, which consists of the African wild dog, the cheetah (*Acinonyx jubatus*), the leopard (*Panthera pardus*), the spotted hyena (*Crocuta crocuta*) and the lion (*P. leo*), thus offers the last opportunity to investigate a complete range of interactions among large predators. Large predators in extant and extinct guilds are known to compete for similar prey species, despite the variation in body size among guild members (Sinclair et al. 2003, Radloff and Du Toit 2004). This body-size variation has led to strong interspecific

dominance hierarchies, resulting in larger members of the guild dominating the smaller ones (Rosenzweig 1966, Maynard-Smith and Parker 1976, Polis and Holt 1992, Palomares and Caro 1999, Woodward and Hildrew 2002, Carbone et al. 1997). Lions and hyenas are, for example, known to kill wild dogs and cheetahs, steal their food, and exclude them from prey-rich areas, whereas wild dogs and cheetahs have little or no influence on the dominant members of the guild (Laurenson et al. 1995, Mills and Gorman 1997, Durant 1998, Gorman et al. 1998, Creel and Creel 2002).

It has been suggested that smaller, sub-dominant species coexist with their larger and more dominant counterparts through temporal partitioning of habitats and resources (Schoener 1974a, Pianka 1974, Durant 1998, Linnel and Strand 2000, Harrington et al. 2009). Temporal partitioning as a mechanism to reduce competition or predation has been suggested, for example, between predators and prey (Sih 1980, Kotler et al. 1993, Ziv et al. 1993) and between the early mammals and the dominant dinosaurs (Crompton et al. 1978, but see Schmitz and Motani 2011). Accordingly, it is widely accepted that lions and hyenas have strongly shaped the temporal niches of wild dogs and cheetahs. In particular, the previously described diurnal and crepuscular activity pattern of wild dogs and cheetahs has commonly been interpreted as a behavioral adaptation to avoid encounters with the predominantly night-active lions and hyenas (Hayward and Slotow 2009).

Direct field evidence for temporal partitioning in African large carnivores is, however, lacking, and there has been no detailed study of activity patterns conducted on all species of the guild at the same time and in the same place. In the only published paper dealing with the topic, Hayward and Slotow (2009) conclude that "top-down effects appear to drive temporal partitioning within the [African] large-predator guild" and that "the remaining members of the guild probably evolved to become active in periods that limit their potential for interaction with lions." In fact, anecdotal observations (Schaller 1979, Creel and Creel 2002) and a more recent study (Rasmussen and Macdonald 2011) suggest

that light availability at night may influence activity patterns of wild dogs and cheetahs, and that nocturnal activity may be more pronounced than previously thought, thus questioning the real role of lions and hyenas in influencing the activity patterns of the two sub-dominant species.

While a critical test of the temporal partitioning hypothesis would involve removing the dominant predators and looking for a change in the behavior of the sub-dominant species, such a study is clearly impractical. Instead, by carrying out a detailed study of activity patterns of a population of sympatric large predators, we aimed to test whether the activity patterns of wild dogs and cheetahs appear to have been primarily shaped by light availability, rather than by avoidance of lions and spotted hyenas. For this purpose, we attached radio-collars equipped with activity sensors to a total of 25 individuals of the four species, in a region of the Okavango Delta in northern Botswana. We first investigated how activity was distributed throughout the 24-hour cycle for all species. Second, we tested if the nocturnal activity patterns were correlated with moonlight availability. A strong positive relationship would suggest that light availability plays an important role in determining activity at night. Third, for wild dogs and cheetahs, we investigated whether there were trade-offs in activity during different periods of the 24-hour cycle. Specifically, we investigated whether increased nocturnal activity resulted in reduced activity on the following day. Trade-offs in activity within the 24-hour cycle would suggest that, when moonlight is sufficient, sub-dominant predators shift their diurnal activities to the night hours, despite the risk associated with a higher likelihood of encountering more dominant members of the guild.

MATERIAL AND METHODS

The African large predator guild

The African large predator guild consists of five species: the African wild dog, the cheetah, the leopard, the spotted hyena and the lion (Hayward and Slotow 2009), which are characterized by a pronounced predatory behavior. The members of the guild vary in body mass ranging from 200 kg (lion) to 25 kg (wild dog), giving rise to a dominance hierarchy where the larger lions and hyenas clearly dominate the smaller wild dogs and cheetahs. In contrast to lions and hyenas, the outcome of interactions between leopards vs. wild dogs and cheetahs is less unidirectional. Leopards have furthermore been shown to be almost equally active during day and night-time and therefore not unequivocally categorized as nocturnal/crepuscular or as diurnal/crepuscular (Hayward and Slotow 2009, McManus 2009). Because leopards are active throughout the 24-hour cycle, they are not likely to bias the behavior of the other species towards or away from any particular time of the day. For this reason they were not included in the study.

Field work

Radio-collars equipped with sensors (VECTRONIC Aerospace GmbH, Germany) specifically designed to record activity data (see below for more detail) were fitted to the study animals (following Osofsky et al.1995, Kock et al. 2006) by a registered veterinarian in compliance with Botswana law. After immobilization, the collared individuals safely re-joined their group showing no signs of distress. Between 2008 and 2010 we monitored the activity of a total of seven wild dogs in five packs, six cheetahs, six hyenas in five clans and six lions in five prides. All four species were found throughout the entire study area. The collared animals ranged over an area of approximately 4,000 km^2 and their territories largely overlapped (Table S1). Throughout the duration of this study, at least two individuals of each species were collared at any time. However, no more than one

individual per social group was collared at any given time to avoid data duplication owing to the collective movement of group members. Data were recorded for a mean of 329 days for cheetahs (range: 217–472 days); 368 days for wild dogs (range: 217–448 days); 416 days for lions (range: 328–486 days) and 432 days for hyenas (range: 310–587 days).

Subdivision of a 24-hour cycle

To investigate activity patterns, we divided each 24-hour cycle into five periods: night, morning twilight, morning, afternoon and evening twilight. These periods reflect the main activity periods for wild dogs and cheetahs (day and twilight) and for lions and hyenas (night and twilight) as currently described in the literature (Hayward and Slotow 2009). Night stretched between the astronomical dusk and dawn, when the sun is 18° below the horizon and sunlight contribution to overall luminosity is nil. The morning twilight started at dawn and ended at sunrise; the evening twilight started at sunset and ended at dusk. The day lasted from sunrise to sunset and the division between morning and afternoon occurred around noon each day (Fig. S1).

Night-time was further divided into seven periods; three periods before midnight, one period across the midnight hour and three periods after midnight. Each period (apart from the midnight period) had an exact duration of 1.2 hours and was therefore directly comparable to the duration of the morning and afternoon twilight periods. Because the overall night length slightly changes over time, we had to adjust the length of the period spanning midnight, which therefore varied slightly in length (± 30 min).

Light availability and Environmental factors

Moonlight intensity, our main predictor variable, was taken as a measure of light availability at night and was defined as the percentage of the lunar disc illuminated (http://aa/usno.navy.mil/data/). Full moon nights and new moon nights were defined when

respectively ≥ 95% and ≤ 5% of the lunar disc was illuminated, giving 4–5 full moon and 4–5 new moon nights per lunar cycle. First quarter and third quarter moon (i.e. half of the moon visible from the Earth's surface) were defined when the percentage of the lunar disc illuminated was between 45% and 55%. We refer to these phases of the lunar cycle as half moon waning and half moon waxing. Since cloud cover reduces available moonlight during the wet season, we only considered data collected during the dry season (April–October) when cloud cover was negligible. Because temperature has been shown to influence activity patterns of carnivore species (Theuerkauf 2009), we obtained records for the study area and used temperature as a covariate in our statistical models. For each day, average temperatures for the five periods of the 24-hour cycle were calculated using the data recorded at 15 minute intervals by a fixed weather station situated in Maun, the town closest to the study area (http://www.jacanaent.com/Weather.htm). Maun lies at the southern edge of the Okavango Delta and is part of the same geo-ecological system as the study site.

Data analysis

The activity data used in our analyses were systematically collected by radio-collars equipped with two motion sensors mounted on the study animals. The two motion sensors continuously recorded activity bursts and summed them over 5-min intervals; a raw data point consisted of the number of activity bursts/5 min (thus the data are continuous, not categorical). To control for the highly pseudo-replicated nature of the raw data, we averaged, for each day, the activity data recorded by each collar over the five periods of the 24-hour cycle. Thus, the dataset consisted of one activity value for night, morning twilight, morning, afternoon and evening twilight, for each day and for each individual. Study animals were followed during day-time and the observed behavior matched with the data collected by the collars at the time of observation. Resting animals usually showed

activity levels of about 5–15 counts/5 min depending on the species, and we included this threshold line in some of our graphs to help visual interpretation of the results.

For the four species, we calculated mean activity values during each period of the 24-hour cycle during full-moon and new-moon days, as well as mean activity values for the seven periods of the night during full-moon, half-moon (waning and waxing) and new-moon days. Periodicity in the nocturnal activity of the four species was analyzed using Fourier spectral analysis, performed using the statistical software R (R Development Core Team 2011). The Fourier algorithm isolates the period of a sinusoidal waveform (e.g. Polansky et al. 2010), and was applied to nocturnal activity values of each individual separately. Because Fourier analysis does not reveal the directionality and strength of the relationship between variables, we analyzed nocturnal activity using linear mixed-effects models (performed using the statistical software GenStat (GenStat Thirteenth Edition 2010)) with moonlight intensity as an explanatory variable. Nocturnal activity, the response variable, was log-transformed to meet the assumptions of normality and homoscedasticity. Animal identity was treated as a fixed effect; night temperature and activity during the previous day-time were entered as covariates; moon cycles and days nested within moon cycles were treated as random effects. We included a first-order auto-regressive error structure when necessary, based on diagnostic plots of residuals.

To further investigate the effects of nocturnal activity on activity levels the following day and to understand how activity was partitioned across the 24-hour cycle, we constructed four additional mixed-effects models with, respectively, morning twilight activity, morning activity, afternoon activity and evening twilight activity as response variables. The activity variables were log-transformed to meet the assumptions of normality and homoscedasticity. For each model, animal identity, moonlight intensity, activity during the previous periods of the 24-hour cycle (e.g. morning twilight activity when analyzing morning activity) and temperature of the respective period were treated as

fixed effects. For both models, moon cycles and days nested within moon cycles were treated as random effects. Model simplification started from a full model and followed a backward selection procedure based on the Akaike Information Criterion (Zuur et al. 2009). Denominator degrees of freedom reported in the text were rounded to the nearest integer. Significance was assessed at $p = 0.01$. Throughout the text, central tendency values are expressed as mean ± 1 s.e.m.

RESULTS

Nocturnal activity of wild dogs and cheetahs comprised, respectively, 25.9 ± 2.1 % (mean ± s.e.m.) and 25.6 ± 3.5 % of the overall diel activity budget, a high value for two species currently described as day active. In contrast, for lions and hyenas nocturnal activity made up 60 ± 2.7 % and 67.9 ± 2.6 % of their respective activity budgets (Tab. 1). In addition, wild dogs and cheetahs conducted roughly half of their total activity (wild dogs: 51.3 ± 1.3 % and cheetahs: 43.8 ± 1.9 %; Tab. 1) during the main activity periods of lions and hyenas (night and twilight). This rather extensive and unexpected overlap between the activity patterns of the subordinate and the dominant carnivores is inconsistent with the idea of strict temporal partitioning.

Mean activity values over the five periods of the 24-hour cycle (night, morning twilight, morning, afternoon and evening twilight) showed significant differences between full moon days and new moon days for wild dogs and cheetahs but not for lions and hyenas (Fig. 1 & Tab. 1). This suggests that the activity pattern of wild dogs and cheetahs changes over a lunar cycle, while the activity pattern of lions and hyenas remains constant and is thus uncoupled from the phases of the moon (Fig. 1 & Tab. 1). On full moon days, about 40 % (wild dogs: 40.4 ± 3.8 %; cheetahs: 39.7 ± 4.4 %) of the total diel activity of wild dogs and cheetahs occurred at night while this figure dropped to approximately 15 % (wild dogs: 15.9 ± 2.2 %; cheetahs: 13.8 ± 2.4 %) during new moon days (Tab. 1). In contrast,

the night-time activity of lions and hyenas did not change between the different phases of the lunar cycle (Tab. 1).

The Fourier spectral analysis showed that the nocturnal activity of six of the seven wild dogs had a main period of 29.17 ± 0.75 days (mean ± s.e.m.) corresponding very closely with the lunar cycle of 29.53 days (Fig. 2 & 3); one wild dog (#4) did not show any periodicity (Fig. 3). Five of the cheetahs exhibited a main period of 30.45 ± 0.49 days (Fig. 2 & 3), while one individual (#3) showed little signature at this wavelength (Fig. 3). In contrast to wild dogs and cheetahs, the nocturnal activity of lions and hyenas showed no relationship with the lunar cycle, although they exhibited shorter activity cycles of a few days (Fig. 2). A fine-scale investigation of the night-time activity between different phases of the lunar cycle showed that wild dogs and cheetahs adjusted their nocturnal behavior according to the presence of the moon in the sky. For example, during a waning moon, when the moon is in the sky during the first half of the night, both species were highly active during the hours preceding midnight (Fig. S2 & S3). With sufficient moonlight, the night activity levels of wild dogs and cheetahs was comparable with activity levels exhibited during the morning twilight on full moon days (compare Fig. 1 with Fig. S2 & S3). In contrast, the activity of lions and hyenas was not related to the presence of the moon in the sky and remained generally constant during the night (Fig. S4 & S5). This further supports our prediction that moonlight intensity, rather than the activity of lions and hyenas, is a major driver influencing the nocturnal activity of wild dogs and cheetahs.

In the linear mixed-effects models, the nocturnal activity of lions and hyenas showed no relationship with moonlight intensity, despite reports that the hunting success of lions increases when the moon is absent or obscured by clouds (Funston et al. 2001, Packer et al. 2011). In contrast, there was a strong positive relationship between wild dog nocturnal activity and moonlight intensity ($F_{1,571} = 231.06$, $p < 0.001$) although one individual (#4) showed no nocturnal activity (interaction term individual by moonlight:

$F_{6,1020} = 4.33$, $p < 0.001$) (Fig. 3). For cheetahs, there was a similar positive relationship between nocturnal activity and moonlight intensity ($F_{1,981} = 164.02$, $p < 0.001$) although one male (#3) showed consistently high levels of activity at night (interaction term individual by moonlight: $F_{5,981} = 6.38$, $p < 0.001$) (Fig. 3). For both wild dogs and cheetahs, the total diel activity remained roughly constant over a lunar cycle and hence showed no relationship with moonlight intensity (wild dog: $F_{1,512} = 0.69$, $p = 0.41$; cheetah: $F_{1,980} = 1.37$, $p = 0.24$). This suggests that wild dogs and cheetahs trade-off and partition nocturnal and diurnal activity according to available moonlight.

To further investigate this suggestion and understand how diel activity was partitioned, we carried out additional analyses for each periods of the 24-hour cycle. For both wild dogs and cheetahs, high levels of moonlight intensity negatively influenced the activity during each period of the following day, with the exclusion of the evening twilight activity of cheetahs (all p-values < 0.001: Tab. S2). For wild dogs, high activity levels during moonlit nights led to decreased activity the following day (except for the evening twilight activity, which was independent of the activity during the previous night; Fig. 1 & Tab. S2). Morning twilight and morning activity showed a positive relationship as did afternoon and evening twilight activity (Tab. S2). Wild dogs thus show three distinct activity periods (night; morning twilight and morning; afternoon and evening twilight) clearly separated by phases of inactivity. The patterns for cheetahs were different: after correcting for differences in activity due to differences in moonlight intensity (Fig. 1 & Tab. S2), we found that levels of activity in adjacent periods showed a positive relationship; hence it seems that, once active, cheetahs remain active over long periods. (Tab. S2). For both species, temperature negatively influenced activity only during the hottest part of the day (i.e. morning and afternoon periods) (Tab.S2).

DISCUSSION

In contrast to previous studies suggesting a high degree of temporal partitioning among African large predators (Hayward and Slotow 2009), our study in the Okavango delta revealed extensive temporal overlap. This was mainly due to the unexpected nocturnal activity of wild dogs and cheetahs – the two species previously regarded as diurnal – and the partly diurnal habits of lions and hyenas. Only for wild dogs and cheetahs was nocturnal activity correlated with the lunar cycle: with sufficient moonlight, both species were considerably active at night and nocturnal activity constituted almost half of the total diel activity on full moon days. It therefore seems that activity patterns of these sub-dominant species are primarily constrained by light availability, rather than by the activities of the larger, dominant species. Our findings support the idea that at the diel level temporal niche partitioning may be a relatively rare event (Schoener 1974b).

Our results conflict with those from the meta-analysis carried out by Hayward and Slotow (2009) who concluded that available studies did not support nocturnal behavior for wild dogs and cheetahs. However, the authors used data from different sites that had been collected opportunistically using a range of different methodologies for different species. In addition, they often assumed that the timing of sunrise and sunset were constant through the year and along a latitudinal gradient. These assumptions can lead to incorrect conclusions, as pointed out by Nouvellet et al. (2011). Although our results are not consistent with the hypothesis that activity patterns of dominant competitors have been the main force shaping the temporal niches of wild dogs and cheetahs, we nonetheless acknowledge that lions and hyenas pose a real threat (Laurenson et al. 1995, Mills and Gorman 1997, Gorman et al. 1998). Playback experiments have for example revealed short-term behavioral modifications in response to the presence of lions and hyenas such as reduced hunting activity and fleeing behavior (Durant 2000, Webster et al. 2011), and

simulation models revealed the sensitivity of wild dog populations to lion predation (Vucetich and Creel 1999).

Only wild dogs and cheetahs showed nocturnal activity patterns that were correlated with the availability of moonlight while the nocturnal activity of hyenas and lions did not vary over the lunar cycle. This raises the question of why good light is a key requirement for activity in wild dogs and cheetahs but not in lions and hyenas. Both wild dogs and cheetahs hunt small and medium-sized antelopes, e.g. impala (*Aepyceros melampus*), and conduct high-speed chases over relatively long distances. During such chases wild dogs can pursue their prey at 40–60 km/h for more than one kilometer and cheetahs reach speeds of over 100 km/h for several hundred meters. Such long, high-speed chases are inherently risky and good light conditions (i.e. during the day and on moonlit nights) and sufficient visibility are likely to be essential to maintain contact with the prey, avoid fatal injuries and increase hunting success (Schaller 1972, Bertram 1979, Creel and Creel 2002, Rasmussen and Macdonald 2011). This cursorial hunting technique is in clear opposition to the ambush hunting technique of lions, whose success increases when the moon is absent or obscured by clouds (Funston et al. 2001, Packer et al. 2011). Different foraging techniques may thus explain the different activity patterns among the species of the guild, and stress the evolutionary importance of bottom-up forces (e.g. prey acquisition) in shaping the behavior of large carnivores.

If lions and hyenas pose a threat to wild dogs and cheetahs, why do they not completely avoid nocturnal activity? One possibility is that they must take every opportunity to catch prey and that they cannot afford to miss exploiting nights with sufficient moonlight. Thus, wild dogs and cheetahs may have evolved short-term visual, auditory and olfactory cues, e.g. fleeing on hearing lion calls, to avoid potentially dangerous situations, rather than completely avoiding being night-active. Neither wild dogs nor cheetahs showed any cyclical pattern in their total diel activity over the course of

a lunar cycle, suggesting that nocturnal activity was not a strategy to increase the overall activity budget. Instead, wild dogs showed clear trade-offs in activity between adjacent periods within a 24-hour cycle. For example, a night with high activity was followed by a morning with reduced activity, implying that nocturnal activity allowed or forced sub-dominant species to rest the next day. We therefore assume that the benefits of nocturnal activity offset the risks of encountering night-active predators and competitors. Indeed, we might expect hunting success to be higher at night because prey animals have a reduced chance of spotting predators under dim light conditions. For example, it is known that hunting success in cheetahs is higher when they can stalk undetected very close to intended prey (FitzGibbon and Fanshawe 1988) and that wolves (*Canis lupus*) are almost twice as successful when hunting on moonlit nights (Theuerkauf et al. 2003). To the contrary, the high levels of activity during early mornings that followed moonless nights, when activity was limited, suggest a behavioral response to an increasing hunger risk.

The influence of moonlight on the hunting behavior of predator species has been widely described for nocturnal species (Horning and Trillmich 1999, Lang et al. 2006), and our results suggest that moonlight can equally influence (allegedly) diurnal species. Understanding and quantifying the energetic budget of single species based on patterns of activity is beyond the scope of this study; nevertheless, on the basis of our findings, it is evident that wild dogs and cheetahs have more time to fulfill their energetic requirements than just a few hours in the morning and in the late afternoon as currently assumed. Further research is thus required to understand the role of each period of the 24-hour cycle for the diel energetic budget as compared to the diel activity budget.

Our findings suggest that the temporal niches of sub-dominant large predator species are only moderately shaped by the need to avoid predation and competition (Schoener 1974b, Lima and Dill 1990, Theuerkauf 200). This is in contrast to findings at other trophic levels, for example, in guilds of herbivore species (Sinclair et al. 2003,

Chesson and Kuang 2008). Sub-dominant large predators must trade off the risk of encountering dominant species against the risk of starvation (e.g. Lima 1988, Roth and Lima 2007) and sub-dominant large predators appear to be mainly "starvation driven". The well-documented positive relationship between the distribution and density of prey species and their predators (e.g. Carbone and Gittleman 2002) further suggests a tight casual association between bottom-up forces and communities of large predators. Additional research in ecosystems characterized by different densities of competitors and prey species will be necessary to better understand the role of top-down and bottom-up forces in shaping animal communities and facilitating coexistence. In contrast to herbivores, large carnivores must invest a lot of energy finding and catching food, as prey are widely scattered, often rare and difficult to catch, and hunting is energy-intensive, time-consuming and often unsuccessful (e.g. Carbone et al. 1999). Given the relative difficulty of catching a meal versus the relatively low likelihood of encountering a dominant species (large predators live at relatively low densities (Carbone and Gittleman 2002)), we conclude that, on moonlit nights, wild dogs and cheetahs prioritize hunting opportunities and success over the need to avoid been hunted and over the possibility of losing their kill. In conclusion, it appears that under favorable light conditions, the benefits of nocturnal activity outweigh the costs of encountering stronger competitors and predators.

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Appendix A

A table showing the spatial range and overlap of the studied animals is available in ESA's Electronic Data Archives.

Appendix B

A table including the detailed mixed-effect models used to investigate partitioning of activity within the 24-hour cycle is available in ESA's Electronic Data Archives.

Appendix C

A figure depicting the division of the 24-h cycle into five periods: morning twilight, morning, afternoon, evening twilight and night can be found in ESA's Electronic Data Archives.

Appendix D-G

Figures showing the detailed night-time activity pattern during four phases of the lunar cycle (full moon, half moon waning, half moon waxing and new moon) for each of the four species studied are available in ESA's Electronic Data Archives.

TABLES AND FIGURES

Table 1: Percentage (± s.e.m.) of activity during the five periods of the 24-hour cycle over an entire lunar cycle and for two different phases of the lunar cycle. 'Partial overlap' is the sum of the activities recorded during the three periods of major lion and hyena activity (night, morning twilight and evening twilight) and shows how much of the diel activity of wild dogs and cheetahs takes place during times of overlapping activity with their two stronger competitors.

		Wild dog	Cheetah	Spotted hyena	Lion
Overall	Night	25.9 ± 2.1	25.6 ± 3.5	67.9 ± 2.6	60.0 ± 2.7
	Morning twilight	11.0 ± 0.9	9.9 ± 1.4	8.1 ± 0.8	7.4 ± 0.7
	Morning	28.7 ± 1.6	34.3 ± 2.1	10.4 ± 1.7	16.3 ± 1.4
	Afternoon	19.9 ± 1.5	21.9 ±1.5	5.0 ± 1.1	9.3 ± 1.8
	Evening twilight	14.4 ± 0.8	8.3 ± 0.7	8.6 ± 0.5	7.9 ± 0.8
	Partial overlap	**51.3**	**43.8**	**84.6**	**75.3**
Full moon	Night	40.4 ± 3.8	39.7 ± 4.4	66.7 ± 2.3	57.7 ± 4.0
	Morning twilight	8.5 ± 0.5	7.1 ± 1.6	9.3 ± 0.4	7.7 ± 0.5
	Morning	21.2 ±2.4	28.1 ± 2.1	10.5 ± 1.7	16.9 ± 2.1
	Afternoon	16.9 ± 1.8	17.2 ± 1.0	4.9 ± 1.2	9.8 ± 2.0
	Evening twilight	13.1 ± 1.3	7.8 ±0.7	8.6 ± 0.6	8.0 ± 0.9
	Partial overlap	**62.0**	**54.6**	**84.6**	**73.4**
New moon	Night	15.9 ± 2.2	13.8 ± 2.4	67.7 ± 2.9	60.9 ± 2.4
	Morning twilight	13.6 ± 1.0	12.3 ± 1.2	7.6 ± 1.3	7.4 ± 0.8
	Morning	32.2 ± 1.9	40.1 ± 2.0	10.8 ± 1.6	14.5 ± 1.4
	Afternoon	21.9 ± 1.9	24.7 ± 1.8	5.0 ± 1.1	9.2 ± 1.4
	Evening twilight	16.3 ±1.3	9.1 ± 0.7	8.9 ± 0.5	8.0 ± 0.8
	Partial overlap	**45.8**	**35.2**	**84.2**	**76.3**

Figure 1: Mean activity values during five periods of the 24-hour cycle for full moon days (full lines) and new moon days (dashed lines). Error bars represent standard errors of the mean. Connecting lines between mean values have been added for visualization purposes. The horizontal dotted line shows the inactivity threshold.

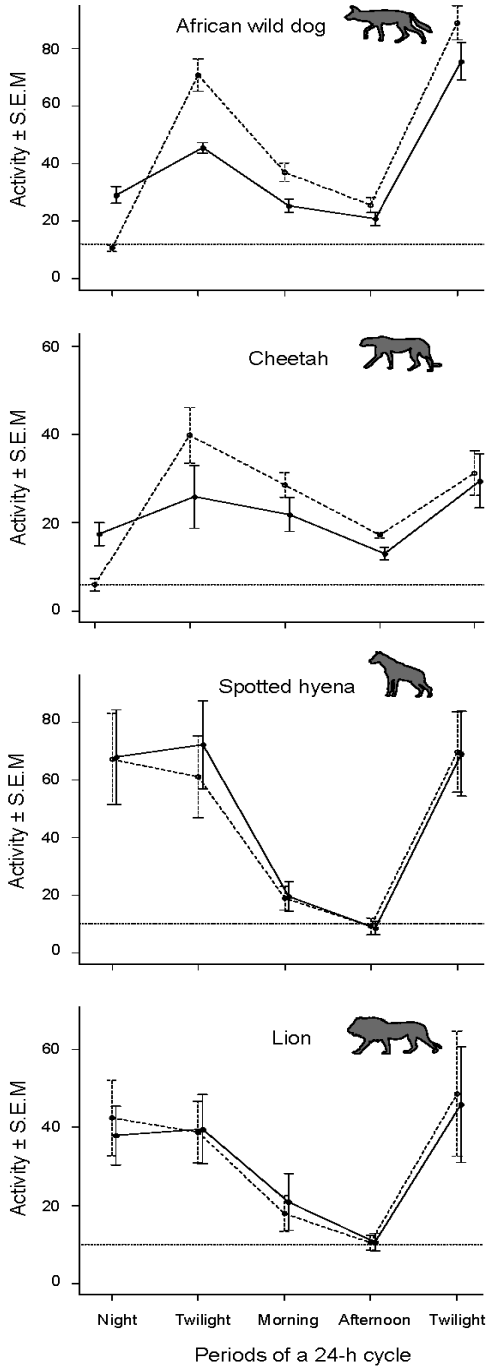


Figure 2: Spectrogram showing periodicity in the nocturnal activity pattern of a typical African wild dog, cheetah, spotted hyena and lion. Activity data recorded by the collars were averaged per night and investigated using Fourier spectral analysis. For comparison the spectrogram of the moon is shown. While the activity of wild dogs and cheetahs shows a main period of 30 days (similarly to the period of the lunar cycle), the activity of spotted hyenas and lions show cyclicity every few days. The width of each peak is a measure of accuracy.

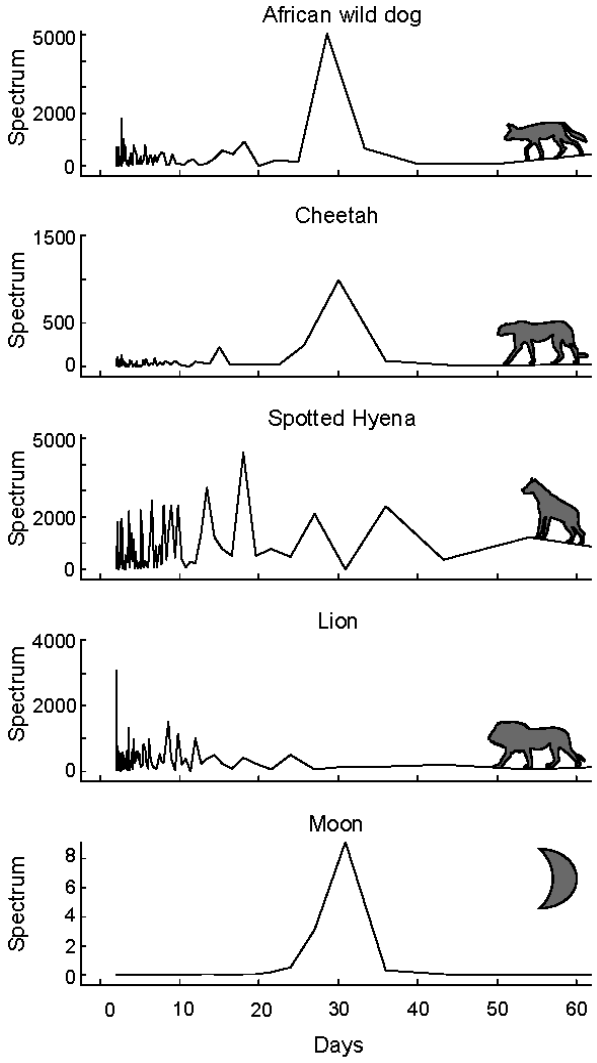
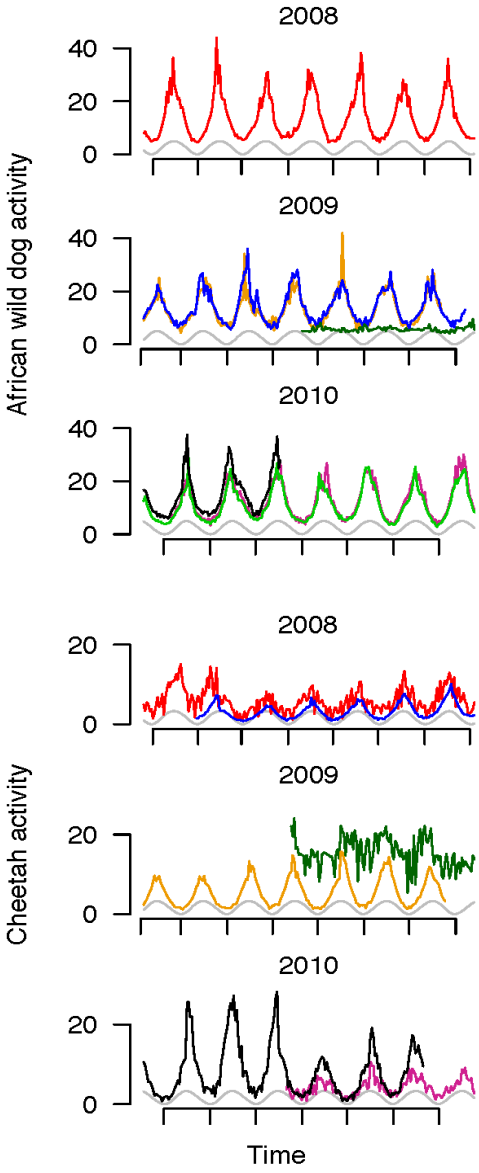


Figure 3: Fitted values from mixed-effects models showing the nocturnal activity patterns of African wild dogs (n = 7) and cheetahs (n = 6) during the dry season in three consecutive years. Each color represents a different individual. Variation in moonlight intensity is depicted for comparison in each panel (grey line; not to scale) and highlights the strong positive relationship between animals activity and moonlight availability. One wild dog (#4, green line) shows no nocturnal activity (2nd panel), while one male cheetah (#3, light green) shows consistently high nocturnal activity (5th panel).



ONLINE SUPPORTING INFORMATION

Appendix A: Total spatial range for the collared individuals of each species (in km^2), and their spatial overlap (in km^2).

		Wild dog	Cheetah	Spotted hyena	Lion
Total range (km^2)		3815	2767	2128	2064
Overlap (km^2)	Wild dog	-	2639	1840	1876
	Cheetah	-	-	1458	1551
	Spotted hyena	-	-	-	1149

Appendix B: Mixed effects models to investigate how the activity in a given period of the 24-hour cycle is influenced by the activity during previous periods. For each case, the best (final) model is given, as well as: the effect of each explanatory variable on the response (positive (+), or negative (-) effect), F-values (F), p-values (p), numerator and denominator degrees of freedom (ndf, ddf). Interactions between explanatory variable are expressed by ':'

AFRICAN WILD DOGS

Morning.twilight.activity ~ Individual+Moon+Night.activity+Individual:Moon

	Ind	Moon	Night	Ind:Moon
effect:		(-)	(-)	
p =	< 0.001	< 0.001	< 0.001	NS
F =	9.95	32.00	47.54	
ndf,ddf =	6,14	1,34	1,360	

Morning.activity ~ Individual+Moon+Morning.twilight.activity+Night.activity+Temperature+

Individual:Morning.twilight.activity+Moon:Temperature+Morning.twilight.activity:Temperature

	Ind	Moon	Mtwl	Night	Temp	Ind:Mtwl	Moon:Temp	Mtwl:Temp
effect:		(-)	(+)	(-)			(-)	(+)
p =	< 0.001	< 0.001	< 0.001	< 0.001	NS	< 0.001	< 0.001	< 0.001
F =	5.50	77.04	467.39	73.25		10.64	18.11	31.56
ndf,ddf =	6,100	1,1204	1,1205	1,1207		6,1204	1,1202	1,1208

Afternoon.activity ~
Individual+Moon+Morning.activity+Night.activity+Temperature+Morning.activity:Temperature

	Ind	Moon	Morn	Night	Temp	Morn:Temp
effect:		(-)	(-)	(-)	(-)	(-)
p =	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.002
F =	6.01	27.74	46.41	24.64	13.34	9.27
ndf,ddf =	6,109	1,613	1,1210	1,1201	1,253	1,1208

Evening.twilight.activity ~ Individual+Moon+Afternoon.activity+Morning.activity+Temperature+
Individual:Moon+ Afternoon.activity:Temperature

	Ind	Moon	After	Morn	Temp	Ind:Moon	After:Temp
effect:		(-)	(+)	(-)	(+)		(-)
p =	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	NS	< 0.001
F =	8.12	15.29	481,04	26.63	20.07		16.16
ndf,ddf =	6;97	1,551	1,1128	1,1207	1,55		1,1130

CHEETAHS

Morning.twilight.activity ~ Individual+Moon+Night.activity+Individual:Moon

	Ind	Moon	Night	Ind:Moon
effect:		(-)	(+)	
p =	< 0.001	< 0.001	0.008	< 0.001

F =	21.29	57.59	7.10	6.51
ndf,ddf =	5,69	1,623	1,983	5,793

Morning.activity ~ Individual+Moon+Morning.twilight.activity+Temperature+
Individual:Moon+Individual:Morning.twilight.activity

	Ind	Moon	Mtwl	Temp	Ind:Moon	Ind:Mtwl
effect:		(-)	(+)	(-)		
p =	< 0.001	< 0.001	< 0.001	< 0.001	NS	< 0.001
F =	9.08	53.22	378.38	17.55		10.91
ndf.,ddf. =	5,62	1,580	1,991	1,54		5.983

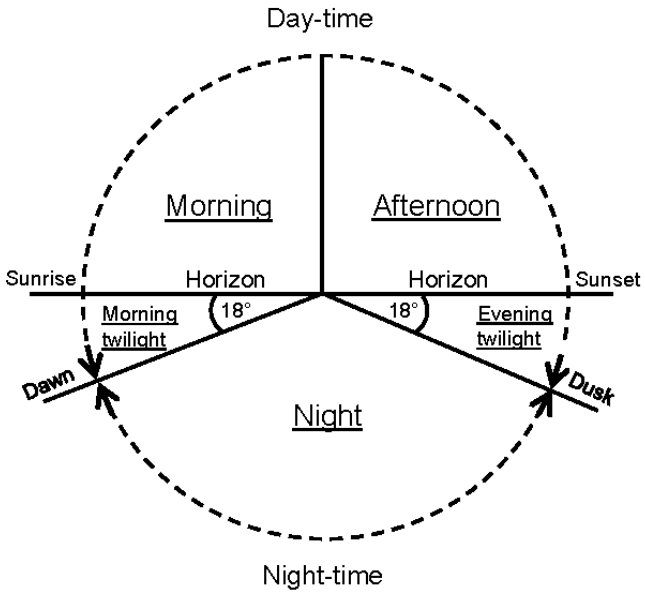
Afternoon.activity ~Individual+Moon+Morning.activity+Temperature+
Individual:Morning.activity+Moon:Morning.activity+Moon:Temperature

	Ind	Moon	Morn	Temp	Ind:Morn	Moon:Morn	Moon:Temp
effect:		(-)	(+)	(-)		(+) (-)	(-)
p =	< 0.001	< 0.001	< 0.001	0.021	< 0.001	0.047	0.004
F =	7.74	38.54	306.29	5.60	4.49	3.96	8.14
ndf,ddf =	5,60	1,990	1,996	1,67	5,993	1,989	1,997

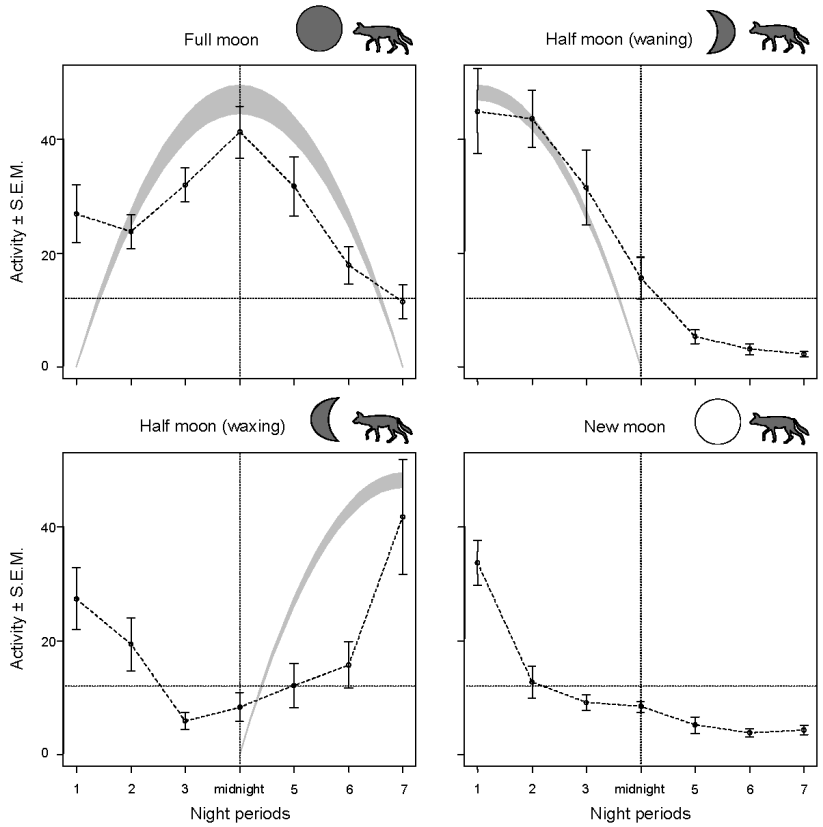
Evening.twilight.activity ~ Individual+Moon+Afternoon.activity+Temperature+
Individual:Moon+Individual:Afternoon.activity

	Ind	Moon	After	Temp	Ind:Moon	Ind:After
effect:			(+)	(+)		
p =	< 0.001	NS	< 0.001	0.043	NS	0.021
F =	23.73		143.43	5.98		2.72
ndf,ddf =	5,12		1,172	1,7		5,185

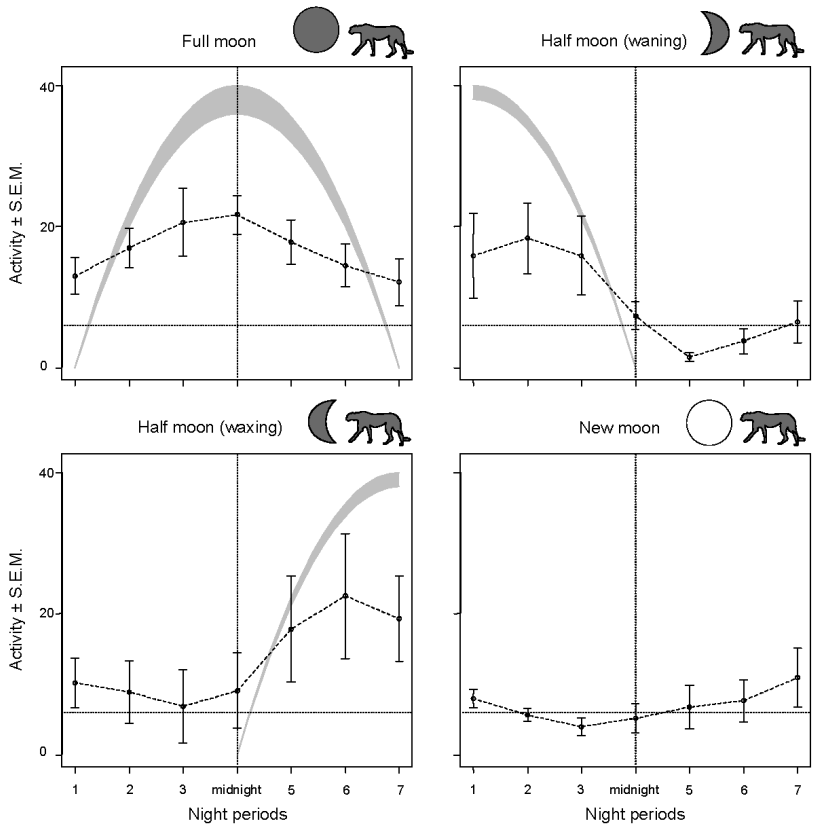
Appendix C: Division of a 24-hour cycle into five periods: morning twilight, morning, afternoon, evening twilight and night. Night-time spanned between the astronomical dusk and the astronomical dawn (sun 18 ° below the horizon) on the consecutive day. The only source of light during night-time is provided by the moon and the stars. Exact times were obtained from http://aa.usno.navy.mil/data/.



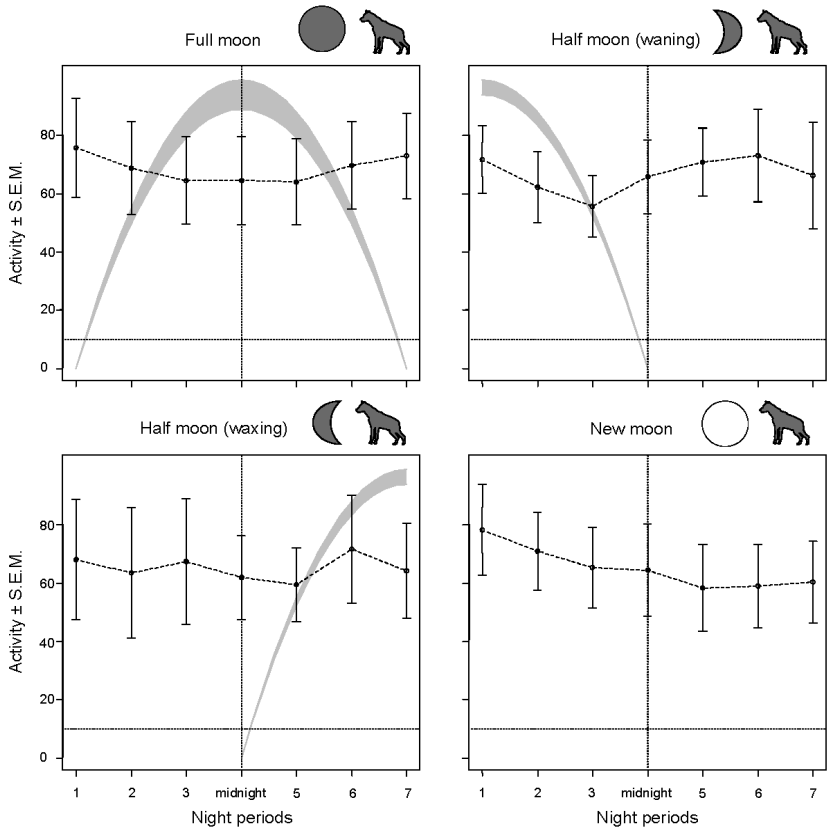
Appendix D: Mean activity values for African wild dogs during seven periods of the night (see text for further details) for four phases of the lunar cycle: full moon, half moon (waning), half moon (waxing) and new moon. The vertical dotted line coincides with the period spanning across midnight. Connecting (dashed) lines between mean values have been added for visualization purposes. The grey curve is a qualitative representation of the trajectory of the moon in the sky; the thickness of the curve qualitatively reflects the intensity of the moonlight as a function of the angle between the moon and the horizon and as a function of the percentage of moon illuminated (i.e. at the zenith the thickness by full moon is twice the thickness by half moon). The horizontal dotted line shows the inactivity threshold.



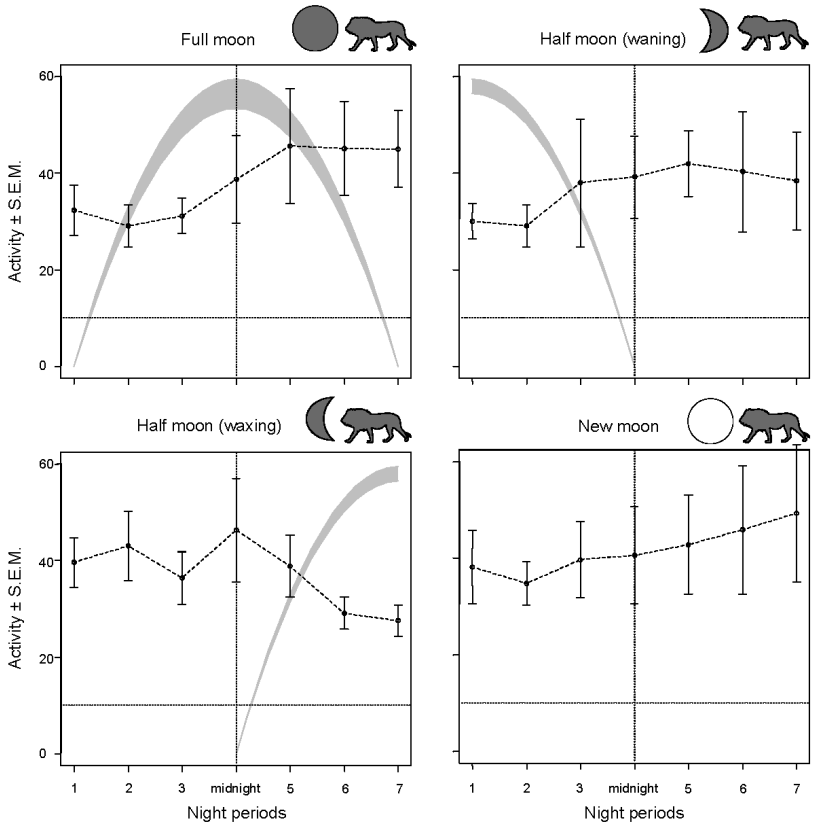
Appendix E: Mean activity values for cheetahs during seven periods of the night (see text for further details) for four phases of the lunar cycle: full moon, half moon (waning), half moon (waxing) and new moon. The vertical dotted line coincides with the period spanning across midnight. Connecting (dashed) lines between mean values have been added for visualization purposes. The grey curve is a qualitative representation of the trajectory of the moon in the sky; the thickness of the curve qualitatively reflects the intensity of the moonlight as a function of the angle between the moon and the horizon and as a function of the percentage of moon illuminated (i.e. at the zenith the thickness by full moon is twice the thickness by half moon). The horizontal dotted line shows the inactivity threshold.



Appendix F: Mean activity values for spotted hyenas during seven periods of the night (see text for further details) for four phases of the lunar cycle: full moon, half moon (waning), half moon (waxing) and new moon. The vertical dotted line coincides with the period spanning across midnight. Connecting (dashed) lines between mean values have been added for visualization purposes. The grey curve is a qualitative representation of the trajectory of the moon in the sky; the thickness of the curve qualitatively reflects the intensity of the moonlight as a function of the angle between the moon and the horizon and as a function of the percentage of moon illuminated (i.e. at the zenith the thickness by full moon is twice the thickness by half moon). The horizontal dotted line shows the inactivity threshold.



Appendix G: Mean activity values for lions during seven periods of the night (see text for further details) for four phases of the lunar cycle: full moon, half moon (waning), half moon (waxing) and new moon. The vertical dotted line coincides with the period spanning across midnight. Connecting (dashed) lines between mean values have been added for visualization purposes. The grey curve is a qualitative representation of the trajectory of the moon in the sky; the thickness of the curve qualitatively reflects the intensity of the moonlight as a function of the angle between the moon and the horizon and as a function of the percentage of moon illuminated (i.e. at the zenith the thickness by full moon is twice the thickness by half moon). The horizontal dotted line shows the inactivity threshold.



Chapter Three

The ecology of fear among African territorial large carnivores: when being afraid of the cat becomes a dog's life. *To be submitted*

Top: Encounters between wild dogs and lions often end with lethal consequences for the dogs. Lions actively kill wild dogs when chances arise and represent up to 50% of the natural causes of mortality (photo courtesy John W. McNutt).

Bottom: A group of African wild dogs mobbing a spotted hyena. Single individuals do not represent a danger for a pack of dogs, however, when more than one hyena aggregate at a wild dogs kill site they frequently succeed in stealing the dog's food

The ecology of fear among African territorial large carnivores: when being afraid of the cat becomes a dog's life.

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Running Headline: The ecology of fear among territorial carnivores

ABSTRACT

The concept of landscapes of fear – i.e. probabilistic utilization maps associated with the likelihood of encountering predators – has largely been applied to investigate prey-predator relationships. In this study we expand this concept and incorporate competition pressure and investigate how territorial carnivore species react to the risk posed by larger, dominant carnivores. Within this framework, we analyzed the spatial distribution of the subordinate African wild dog *Lycaon pictus*, in relation to 1) the landscapes of fear created by the dominant spotted hyena *Crocuta crocuta* and lion *Panthera leo* (top-down forces), and 2) prey distribution and abundance, vegetation type and distance to water sources (bottom-up forces). We collected data from a total of 40 individuals fitted with GPS radio collars. We found a negative relation between the likelihood of encountering wild dogs and the likelihood of encountering lions, suggesting a density threshold above which the subordinate wild dogs are excluded from an area by their larger and stronger competitors and predators. However, wild dogs did not consistently avoid those vegetation types, which were selected by lions and hyenas. The use of space by wild dogs was thus mainly driven by top-down forces rather than by bottom-up forces. Our findings further suggest that the distribution of risks plays an important role in shaping the size and boundaries of a territory as well as the use of the space within such territory. We conclude that spatial avoidance, both on a between- and within-territory scale, facilitates coexistence among members of the large predator guild by reducing direct encounters.

Key-words: Carnivore-carnivore interaction; coexistence; habitat use; landscapes of fear; spatial segregation

INTRODUCTION

It is widely accepted that the distribution of animal species in space and time results from a trade-off between minimizing the risk of predation and competition (top-down forces) and maximizing resource acquisition (bottom-up forces) (Sih 1980, Mangel and Clark 1986, Brown and Kotler 2004). Fundamental for the understanding of how animals utilize their environment is therefore an accurate qualification and quantification of the top-down and bottom-up forces involved. However, whereas resources can be fairly easily qualified and quantified (e.g.: amount of fruit per hectare, Willems and Hill 2009; distribution of waterholes; Valeix et al. 2009), thus allowing ecologists to relatively easily investigate the effect of bottom-up forces on the distribution of animals, risks are often intrinsic of an animal's perception and understanding of the surrounding landscape and difficult to qualify and quantify.

In the past, indirect cues such as vigilance or alarm calls have been used as a proxy to assess perceived risk of predation (Brown et al. 1999, Willems and Hill 2009). Yet an animal's *perception* of risk does not necessarily reflect the *real* distribution of the latter. In order to understand whether animals have the ability to objectively assess and even predict the spatio-temporal distribution of risks or the availability of resources—in other words to understand the cognitive capacity of an animal with regard to its surrounding environment—the real risks and the distribution of resources need to be empirically quantified (Valeix et al. 2009). Incorporating risks and resources within a framework of landscapes of fear—i.e. probabilistic utilization maps, associated with the likelihood of encountering predators and originally developed to investigate the distribution of herbivore prey species (Brown et al. 1999)—will help clarifying the evolutionary importance that several factors have in shaping the behavioral, phenological and morphological traits of animal species.

Following a three-trophic-level (plant–herbivore–carnivore) assumption, carnivore species have long been considered as predators only and assumed to be under no, or limited, risk of predation (Mukherjee et al. 2009). Their distribution and use of the environment has thus often been explained solely by the distribution of their prey resources (Macdonald 1983, Sih et al. 1998). Only more recently the concept of fear has, for instance, been used to investigate the effect of larger carnivores on co-occurring mesopredators (Berger and Gese 2007, Mukherjee et al. 2009). This approach, however, has never been applied to larger carnivores. A crucial aspect, which will have to be taken into consideration in the context of the ecology of fear, is that the majority of large carnivores are territorial and thus restricted in their movements by the presence of neighboring groups of conspecifics. Therefore, avoidance of risks will have to occur within well-defined, exclusive territories and strategies to minimize the negative effects of risk may be different from those used by species that can range freely like the majority of the herbivore species. We anticipate that risk will be an important force shaping the within-territory use of space in territorial species.

Within this framework, the main aim of this study is to investigate how large, territorial, subdominant carnivores react to the risk posed by other large carnivores. We addressed this question focusing on a population of free-ranging, territorial carnivore species: the African wild dogs *Lycaon pictus*, the spotted hyena *Crocuta crocuta* and the lion *Panthera leo*. An asymmetric dominance hierarchy where the larger lions dominate the smaller spotted hyenas and both in turn dominate the smaller wild dogs characterizes the three species. Lions and hyenas have been shown to negatively influence wild dog populations through predation and direct competition (Creel and Creel 1996, Woodroffe et al. 1997, Creel and Creel 1998, Gorman et al. 1998). Accordingly, across several ecosystems, the density of wild dogs has been shown to negatively correlate with the density of lions and spotted hyenas (Creel and Creel 1996). Subdominant species may,

however, coexist with their stronger competitors and predators seeking spatial refuge and segregation by means of habitat partitioning (Pianka 1974, Schoener 1974, Levine 1976, Durant 1998, Linnell and Strand 2000, Holt and Barfield 2003, Harrington et al. 2009, Levine and HilleRisLambers 2009). A deeper understanding of how the species interact on a smaller, within-territory spatial scale is nevertheless fundamental to understand density thresholds at which interspecific competition may play an exclusion role. Here we analyzed the spatial distribution of a competitively subordinate species, the wild dog, in relation to 1) the landscape of fear created by its stronger competitors (top-down forces), and 2) prey distribution and abundance, vegetation type and distance to water sources (bottom-up forces).

MATERIAL AND METHODS

Study area

This study was conducted in the Okavango Delta in Northern Botswana, over an area of approximately 4'000 km^2 that comprised the south-eastern section of Moremi Game Reserve (MGR) and the adjacent Wildlife Management Areas (WMAs) north of a veterinary cattle fence (Fig. 1). The Okavango Delta is a freshwater ecosystem characterized by a mosaic of habitat types, such as rivers, swamps, perennial floodplains, seasonal floodplains, grasslands, shrubby grasslands, grasslands dominated by *Acacia* spp., woodlands dominated by mopane (*Colophosperum mopane*) and riparian woodlands (Mendelson et al. 2010). The different habitat types support different prey species and density (Bartlam 2010; G. Cozzi unpubl. data). The region is characterized by a dry season between April and October and a wet season between November and March with an average precipitation of 450–600 mm/year (Mendelson et al. 2010).

Fieldwork and data collection

We systematically recorded GPS location data on individual African wild dogs, spotted hyenas and lions using programmed GPS radio-collars (Vectronic Aerospace GmbH, Germany). In compliance with Botswana law, target animals were immobilized for collaring purposes by a qualified wildlife veterinarian using approved techniques and drug combinations (Osofsky et al. 1996, Kock et al. 2006). After immobilization, the collared individuals safely re-joined their groups showing no signs of distress. The data presented here are from eight wild dogs in five packs, 15 spotted hyenas in seven clans and 17 lions in eight prides. Between 2007 and 2010, a mean of 1,011 locations (range: 398–1444) were recorded for individual wild dogs, 2,747 locations for hyenas (range: 395–9450) and 2,951 locations for lions (range: 223–7307).

The collars were scheduled to record several GPS locations per day. For wild dogs, GPS locations were recorded at 06:00, 12:00 and 18:00; for hyenas and lions, one location was recorded every two hours between 18:00 and 06:00 and one location was recorded at noon, giving a total of eight GPS locations per day. On average, collars successfully recorded 84.8 ± 3.2 % (mean ± s.e.m) of the scheduled locations. In a test, 14 randomly selected collars were placed at known GPS locations under thick canopy cover and the distance between each GPS location collected by the collars and their actual location was measured in ArcGIS 9.2 (ESRI, United States). The GPS locations (n = 246) collected by the test collars were used to predict their accuracy, which was 11.6 m ± 4.0 m (mean ± s.e.m), and was assumed to be representative for the accuracy of all collars deployed in the field.

Landscape matrix parameters

Each location within the landscape matrix, i.e. the landscape through which animals move, was characterized by a range of attributes such as vegetation type, vegetation cover, prey

distribution, physical traits such as distance to perennial water sources and the risk associated with the likelihood of encountering intra- and interspecific competitors (landscape of risk) (Fig. 2 and Fig. S1).

Vegetation map: A vegetation map was created based on two SPOT5 multispectral satellite images with a 30 x 30 m (pixel) spatial resolution, acquired in October 2009 (end of the dry season). The images were pre-processed in ENVI 4.8 using provided calibration factors, the atmospheric correction tool FLAASH, and mosaicking. Corrected images were classified based on a support vector machine model trained with 9 classes using reference coordinates acquired in the field. Resulting classes were merged to five final major vegetation types (Fig. 2A and Fig. S1): 1) floodplains, which included rivers, swamps and perennial floodplains; 2) grass, which included seasonal and ephemeral floodplains, short grass savannah and bare soil and characterized by the absence of trees and shrubs; 3) mixed acacia, which included acacia savannah and denser acacia mixed woodland and characterized by the presence of evergreen *Acacia* spp.; 4) riparian, which was characterized by riverine vegetation growing on elevated ground along extant or ancient channels and floodplains; and 5) mopane woodland, which was characterized by the almost exclusive presence of *Colophospermum mopane*. Following ground-proofing, the overall accuracy of the final vegetation map was 72.4%. One of the five vegetation classes was thus assigned to each pixel within the study area. Additionally, the distance between the centre of each pixel and the closest perennial water source (natural or artificial) was calculated in ArcGIS 10.0 (by ESRI). For a further description of the vegetation types and the creation of the vegetation map see the Online Supporting Information.

NDVI and prey density map: A digitalized map representing NDVI values was created based on two SPOT5 multispectral satellite images (see above). We used high NDVI values to highlight photosynthetically active vegetation, which during the dry season when the satellite images were acquired was represented by evergreen *Acacia* spp.,

riparian tree species associated with underground water and inundated floodplains. These vegetation types were in clear contrast with leafless mopane and dry grasslands that showed very low NDVI values (Fig. 2B and Fig. S1). Ground surveys in the study area showed that impala (the preferred prey species of wild dogs) density was highest in acacia woodland and riparian or floodplains and lowest in mopane and grassland (Bartlam 2010, Broekhuis et al., pers. comm.). The NDVI values where thus categorized into a high and a low group and these groups were used as a proxy for high versus low impala density.

Habitat physical structure: We further classified the landscape matrix according to its physical structure, as we were interested in evaluating different levels of visibility between habitat types. Visibility likely plays a major role in the detection, respectively concealment, of animals, thus potentially influencing habitat selection and use. However, because within vegetation classes, visibility scores varied considerably, visibility could not be used in further analyses linking visibility to habitat type (Fig. S2). A detailed description of the methodology used to assess visibility is, however, available in the Online Supporting Information.

Utilization distribution map and landscape of risk

Utilization or probabilistic distribution maps for African wild dogs, spotted hyenas and lions (Fig. 2C-F), were created through Gaussian kernel density estimation (KDE) in the Geospatial Modelling Environment (GME, Version 0.6.0.0). The least-squares cross-validation (LSCV) method was used to parameterize the kernel bandwidth. Isopleths representing the 50, 90, 95 and 99 % volume of the distribution maps were subsequently calculated and used to define four levels of home-range size commonly used in the literature (Harris et al. 1990, Willems and Hill 2009, Fieberg and Börger 2012). This information was then used to investigate habitat use and vegetation preferences (see below).

Spatially inclusive and comprehensive information on spotted hyena and lion distributions was only available for one group of African wild dogs (Mathew's pack; Fig. 2F), which completely overlapped with five spotted hyena clans and six lion prides. For the territory occupied by the Mathew's pack (1,531 km^2, 99 % kernel), a species-specific probabilistic landscape of risks of spotted hyenas (Fig. 2C), lions (Fig. 2D) and neighboring wild dog groups (Fig. 2E) were also created through weighted KDE using LSCV parameterization. To assure that the utilization maps would not be biased by the 'sampling effort' (i.e. number of GPS locations/individual), the same number of locations per individual (within each species) were used to calculate the landscapes of fear. Because the risk associated with the likelihood of encountering competitors also depends on their group size, the weighted KDE were calculated with group size as weighting factor.

Data analysis

The dataset combined several geographic layers containing layer-specific information (e.g. vegetation type), stacked over each other. Between layers, pixels were linked to each other through X and Y Cartesian coordinates (Fig. S3). Animal locations from the GPS collars were laid on top of the geographic layers.

In a first step we analyzed habitat use at a *within study area* spatial scale. We investigated, for the three species, the amount of each vegetation type within the territory of each individual (W) in relation to the amount of vegetation type available within the entire study area (A) (Johnson 1980). A selectivity index defined by the formula

$$I = \frac{W - A}{W + A}$$

was chosen to analyze the exploitation of a resource in relationship to its availability (for an overview see Chesson 1978). Standardized values varied from –1 to +1 representing

under-representation versus over-representation of a particular habitat type within the territory of an animal.

In a second step, we analyzed habitat selection on a *within territory* spatial scale by comparing the percentage of GPS locations falling within each vegetation type to the percentage of each vegetation type available within the territory of each individual. We used linear models and tested against the null hypothesis of a non-difference from a slope of 1, which represents a perfect correlation between the use of a habitat and its availability. Regression lines were forced through the origin and based on the Aikaike Information Criterion (AIC) performed better than models with free intercept.

Integrating bottom-up and top-down forces in the landscape of fear framework

We investigated the within-territory spatial patterns of the Mathew's pack (Fig. 2F)—the only group for which comprehensive information on all explanatory variables was available—as a function of the risk of encountering lions (Fig. 2C) and spotted hyenas (Fig. 2D), of the distribution of neighboring wild dogs (Fig. 2E), of five distinct vegetation types (Fig. 2A) and prey abundance (Fig. 2B) and of the distance to the closest perennial water source. The methodology followed the conceptual framework outlined in Willems and Hill (2009). A grid composed of 2.5 by 2.5 km quadrats was overlaid on the territory of the Mathew's pack and the pixel values—of the response variable and of explanatory variables—corresponding to each vertex of the quadrats were extracted (N = 198). The size of the quadrats was set to represent the average distance moved by wild dogs between two consecutive locations (mean ± s.e.m.: 2.64 ± 0.05 km) and thus to avoid introducing unnecessary spatial autocorrelation in the data. It is important mentioning that equal pixel values for the risk associated with lions, hyenas and neighbouring dogs do not represent an equal absolute risk as lions are for example potentially more dangerous than the other two species.

Despite our precautions, because of the nature of the data, both the response variable and the explanatory variables showed a certain degree of spatial autocorrelation. Since the response variable—i.e. the likelihood of finding the Mathew's pack on a particular location (any of the 198 pixel values)—heavily departed from a normal distribution and because it could only take on values between 0 (= locations at the edge the dogs' territory with a very low chance of finding them) and $y_{max} < 1$ (= locations in the center of the dogs' territory where there is a high chance of finding them), commonly used spatial auto-regressive models (e.g. SAR) that assume a Gaussian distribution (Kissling and Carl 2008) could not be used. Instead, a beta distribution with logit link function was used to alleviate heteroscedasticity and skewness. A beta regression can be understood similarly to a generalized linear model but provides more flexibility when the trials are not independent (Cribari-Neto and Zeileis 2010). The best model was selected following a backward selection procedure based on the AIC criterion (Zuur et al. 2009) and the adequacy of the model was visually investigated looking at the spatial distribution and autocorrelation of the model residuals (Willems and Hill 2009).

RESULTS

Habitat selection

To test for habitat preference and avoidance we explored two types of habitat selection. 1) Habitat availability, which investigates the amount of a particular habitat type within an animal's territory in relation to its availability within the entire study area and 2) Habitat use, which investigates the time that an animal spends in a particular habitat type in relation to its availability within the animal's territory.

We compared the amount of each of the five vegetation types within the territory of each individual ($N_{wild\ dogs} = 8$, $N_{hyenas} = 15$, $N_{lions} = 17$ individuals) with the amount of vegetation type available within the entire study area. There was, on average, less

floodplain and riparian within the territories of the three species than available within the study area, and this was particularly true for wild dogs and spotted hyenas (Fig. 3). This suggests that these vegetation types where less accessible, probably due to high water. The amount of mopane forests within the territory of lions and, to a lesser extend spotted hyenas was considerably lower than the amount of mopane forests available within the study area (Fig. 3). The amount of mixed acacia woodland, grassland and mopane forest within the home ranges of wild dogs reflected, however, the overall availability, indicating a substantial degree of flexibility and adaptability to different habitat types (Fig. 3).

Wild dogs used grassland more ($t_{1,7}$ = 3.05, p = 0.02, slope: a = 0.31) and floodplain less often ($t_{1,7}$ = –20.73, p < 0.001, a = –0.94) than expected by chance. The horizontal relationship between the use of floodplains and the percentage of this habitat within territories suggested a consistent avoidance of floodplains (Fig. 4). Spotted hyenas ($t_{1,14}$ = –15.02, p < 0.001, a = –0.69) and lions ($t_{1,16}$ = –1.83, p = 0.08, a = –0.23) showed a similar avoidance for floodplains, and this is distinguishable by the respective correlation lines in Fig. 4, which are below the identity line that indicates that a habitat is used according to its availability. However, the correlation between the use of floodplains and its availability was positive, suggesting that those individuals inhabiting wet areas got used to, and made limited use of it (Fig. 4). Similarly to what we observed for the habitat availability analysis (see Fig. 3), lions selected acacia ($t_{1,16}$ = 3.99, p = 0.001, a = 0.16) and avoided mopane woodland ($t_{1,16}$ = –7.98, p < 0.001, a = –0.28) (Fig. 4). In other words, they spend a considerable amount of time in acacia and little time in the mopane forests. We did not detect any significant difference in the use of the habitat types between the dry and the wet season for wild dogs and hyenas, while season significantly influenced the habitat use of lions (interaction term vegetation by season $F_{1,9}$ = 3.19, p = 0.01). In particular, lions used riparian and floodplains considerably less, and mopane considerably more often during the wet season than during the dry season.

For wild dogs, the focal species of this study, we further analyzed the percentage of locations falling within each vegetation type for four discrete territory isopleths (50, 90, 95 and 99 % kernel) but did not find any significant differences. In other words, there was not a particular habitat type preferred within (say) the 50 % isopleth compared to (say) the 90% isopleth as one may expect following the assumption that a particular vegetation type may be considered as a safer refuge and therefore likely "over-represented" in the core area of an animal's territory (i.e. where it spends most of its time).

Integrating bottom-up and top-down forces

Distribution data from one group of wild dogs (Mathew's pack) whose territory completely overlapped with the territory of six groups of lions and five groups of spotted hyenas and which was surrounded by three neighboring groups of wild dogs were used to investigate the determinants influencing the within-territory use of space by wild dogs.

Beta regression models showed that the core area of the territory (50 % kernel isopleth) of the Mathew's pack was characterized by a significantly lower risk of encountering lions and neighboring packs of dogs than the outermost isopleths (Fig, 5, Tab. 1). This suggested that the core area represents a relatively safe area with a reduced risk of intra- and interspecific interactions. The same area, in contrast, was characterized by a high likelihood of encountering spotted hyenas and this may indicate a casual positive association influenced by resource selection, rather than a direct association between the two species (Fig. 5, Tab. 1).

The utilization of the territory by the Mathew's pack showed a negative relationship with the risk associated with lions ($z = –2.62$, $p = 0.009$) and neighboring packs of dogs ($z = –5.82$, $p < 0.001$) but a positive relationship with the risk associated with spotted hyenas ($z = 6.54$, $p < 0.001$) and the presence of perennial water ($z = 2.93$, $p = 0.003$). Vegetation type and NDVI did not show any significant relationship with territory utilization by dogs.

Overall the model explained about 35 % of the variance of the data (Pseudo R-squared = 0.351). This relatively low explanatory power and the fact that the spatial structure of the data could not be entirely captured by means of the recorded explanatory variables (as visually shown by the spatial structure of the residuals, Fig. 6) suggest that additional explanatory variable may shape within-territory habitat use in wild dogs.

DISCUSSION

We applied the concept of a landscape of fear—originally developed to investigate the distribution of prey species in relation to the distribution of risks associated with their predators (Brown et al. 1999)—to a large territorial carnivores species, the African wild dog, living under competition and predation pressure by the larger spotted hyenas and lions. Our results suggest a density threshold above which the competitively inferior wild dogs are excluded from an area by their larger and stronger competitors and predators, thus supporting the idea of a density-related coexistence mechanism. In our study this was illustrated by the negative relationship between the likelihood of encountering wild dogs and the likelihood of encountering lions (distribution of risk) (see Fig. 5, 6). Our findings, that apply on a within-territory scale, thus expand on the findings by Creel and Creel (2002) who showed a negative correlation between wild dog density and lion density across ecosystems.

This suggests that wild dogs have the ability of objectively assess, and possibly predict, the real distribution of risks, and accordingly adjust the use of their territory to minimize such risks. Predation by lions is the first natural cause of mortality in wild dogs, accounting for 50 % of the recorded cases (in Woodroffe et al. 1997), and avoiding risky areas (i.e. areas characterized by a high likelihood of encountering lions) may be a strategy to enhance survival. In contrast, we could not detect any negative relationship between wild dogs and spotted hyenas supporting the idea that in the study area, like in other

similar ecosystems, hyenas have little or no direct effect on the spatial behavior of wild dogs (Creel and Creel 2002, Webster et al. 2010, 2012). It remains to be analyzed which mechanisms and cues animals use to discriminate between high- and low-risk areas. Such cues may be acoustic, olfactory or depend on direct experience.

Our results are in contrast to the behavior of cheetahs inhabiting the study area, which in spite of competition and predatory pressures from lions and hyenas do not avoid areas with high likelihood of encountering these two top predators (Broekhuis et al., pers. comm.). This difference may be explained by the low territoriality of cheetahs compared with the highly territorial wild dogs. Non-territorial species may use a risky area under particular conditions because they can, at any time, move elsewhere when needed (e.g. when attending young cubs at a lair). Territorial species, in contrast, are confined within their territory and therefore certain minimal conditions have to be met to "settle down". The establishment of territory boundaries that need to be patrolled and defended against intruders is a costly task and it is an evolutionary disadvantage to invest energy in defending an unsuitable, risky area that therefore might remain completely vacant. In accordance with Creel and Creel (1996), we see in the large territories of wild dogs the necessity to have areas with differential levels of risk where to retreat when necessary (e.g. during the denning period).

Our findings further suggest that the distribution of risks can play an important role in shaping the size and boundary of a territory as well as the within-territory use of the space. The unusual shape of the territory of the Mathew's pack may indeed be the consequence of a high lion risk in the north-western part of the dogs' range (Fig. 2C & 2F). This unexpected shape is in clear contrast with a theoretical circular shape that maximizes the area-to-perimeter ratio and that one would expect in the absence of shaping forces. Risk is probably one element among several in shaping the territory of an animal and its use, and conceivably interacts with the abundance and distribution of prey and the presence

of conspecific neighbors (Berger and Gese 2007, Berger et al. 2008). Similarly, within their territory, wild dogs established the core area (represented by the 50 % kernel isopleth)—typically the most sensitive area where animals spend most of their time—to coincide with a very low risk of encountering lions. In the study area, wild dog den sites occurred within the core area and this may be indicative of the negative pressure exerted by lions. The area in the northwest consistently avoided by the Mathew's pack coincided with the territories of two prides of lions numbering more than 15 individuals and thus close to a density that can confidently be estimated at > 15 lions/100 km^2. Areas above this threshold may become too risky and unsuitable to establish a permanent territory; no other packs used this area either. This result supports the conclusion by Creel and Creel (1996) that conservation of wild dogs may be best achieved in areas with a relatively low presence of lions.

Contrarily to what would be expected following the spatial refuge hypothesis (Durant 1998), wild dogs did not consistently avoid or select habitat types, which were selected or avoided, respectively, by lions and hyenas. For predator species that partially rely upon the same prey (Mills and Biggs 1993, Hayward and Kerley 2005, Hayward et al. 2006a, Hayward 2006, Hayward et al. 2006b, Hayward et al. 2006c), their use of the territory may be heavily influenced by the distribution and the habitat preferences of their common prey, thus resulting in a similar pattern of habitat use. The only consistent pattern, both at the between- and the within-territory level, was the underutilization of floodplains and other inundated areas by wild dogs and spotted hyenas and the underutilization of the mopane forest by lions. Indeed, these results underline the importance of these two habitat types in the dynamics of the Okavango Delta ecosystem (Cozzi et al. in pres, Cozzi et al. pers. data). Despite not actively selecting for mopane woodland, wild dogs appeared to be equally capable to exploit this habitat type and survive within large patches of mopane, clearly avoided by lions and therefore characterized by a lower risk. In fact, further data

(not shown) indicated the importance of mopane woodland for the location of den sites; and direct field observations hinted towards an increased hunting success of wild dogs in wooded habitats (as compared to completely open grasslands), where fleeing prey could get obstructed by the vegetation (Creel and Creel 2002, G. Cozzi, pers. obs.). The physical structure (e.g. visibility or tree density) of the habitat type may thus play an important role in explaining the spatial patterns of animal species and efforts should be made to incorporate such information with the analyzed variables.

We showed how the risk posed by dominant species (top-down effect) can influence the spatial ecology of competitively inferior species of the same guild, shape territory size and territory boundaries and mediate coexistence. A recent study found a reduced degree of temporal partitioning among large African carnivore species (Cozzi et al. in press). Thus, spatial avoidance, both on a between- (Creel and Creel 1996) and within-territory scale (this study), rather than temporal partitioning, may play a major role in reducing direct encounter rates between guild members, facilitating coexistence between these large carnivores (Schoener 1974). Such situations may particularly apply to territorial species that are restricted in their ranging behavior by neighboring conspecifics. To our knowledge, the present study is the first to investigate the distribution of a territorial large predator species by simultaneously incorporating top-down forces (i.e. competitors and conspecifics) and bottom-up forces (i.e. environment characteristics and prey distribution) within the framework of the ecology of fear. Our research illustrates the great potential for such a holistic and multi-species approach and highlights two aspects that will need to be considered in the future: the role of territoriality in influencing interspecific interactions and the ecology of fear, and how differential levels of risk and the associated concept of fear influence activities and behavior in subordinate species.

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TABLES AND FIGURES

Table 1: Summary table of three beta regression models of risk as a function of four discrete isopleths (50, 90, 95 and 99 % kernel) commonly used in ecological studies investigating animal territoriality. * Coefficients are calculated via a logit function and can be back-transformed to the original scale using the inverse logit function: $\text{logit}^{-1}(\alpha) = \exp(\alpha)/(1 + \exp(\alpha))$. Isopleths have been used as predictors for the evaluation of the precision parameters (not shown).

	Isopleth	Estimate of risk*	Std. Error*	Z-value	P-value
Lion	50%	-5.996	0.097	-61.67	< 0.001
	90%	0.842	0.136	6.20	< 0.001
	95%	1.091	0.193	5.66	< 0.001
	99%	0.598	0.186	3.21	0.001
Hyena	50%	-4.558	0.087	-52.19	< 0.001
	90%	-0.573	0.134	-4.29	< 0.001
	95%	-1.517	0.264	-5.75	< 0.001
	99%	-1.378	0.252	-5.47	< 0.001
Wild dog	50%	-6.248	0.316	-19.75	< 0.001
	90%	0.421	0.413	1.02	0.308
	95%	1.092	0.444	2.46	0.014
	99%	1.514	0.338	4.01	< 0.001

Figure 1: The study area in the Okavango Delta, Northern Botswana. The red circle highlights an area of approximately 4,000 km² where several individual African wild dogs, spotted hyenas and lions were fitted with GPS radio collars. The Okavango River and its perennial floodplains are depicted in dark blue and light blue, respectively. Moremi Game Reserve is shown in green and is surrounded by Wildlife Management Areas (white) north of the Buffalo fence (ticked line).

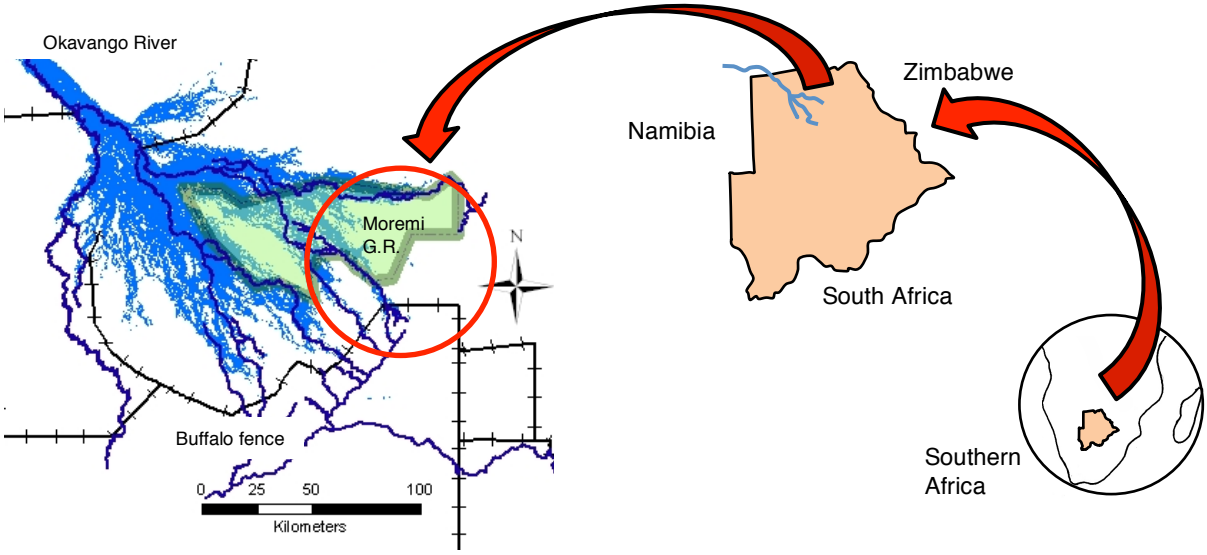


Figure 2: Maps representing predictor variables (A–E) used to describe the spatial distribution of a pack of wild dogs (F). See text for further details.

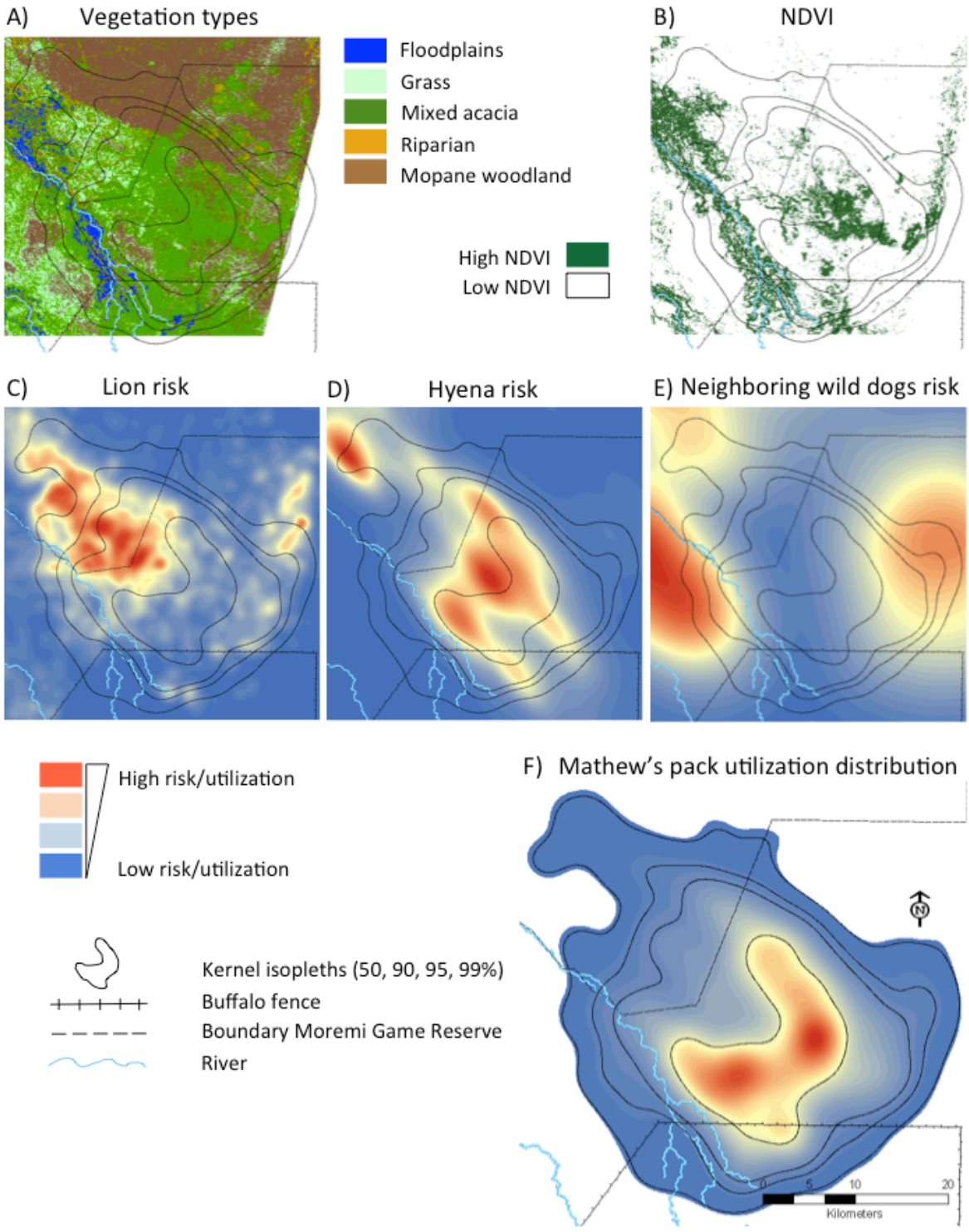


Figure 3: Relationship between the amount of five vegetation types within the territories of eight wild dogs, 15 spotted hyenas and 17 lions, and the amount of available vegetation in the overall study area. The 0-value on the vertical axis (dotted line) means that, within a territory, a vegetation type was represented in accordance to its availability within the study area; positive values represent over-representation and negative value under-representation. Confidence bars represent standard errors of the mean calculated on the raw data.

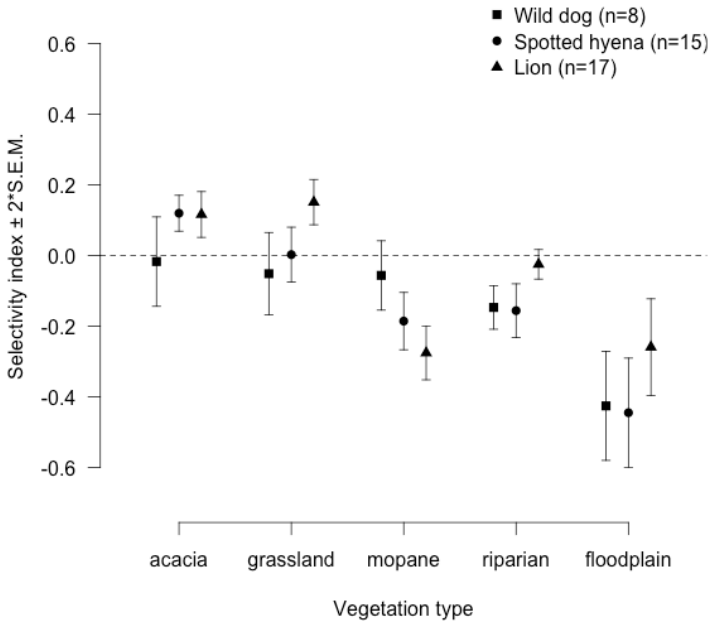


Figure 4: Use of different habitat types as a function of their availability within the territory of wild dogs, spotted hyenas and lions. The red thin line indicates that a habitat is used according to its availability. Lines below and above this line indicate, respectively, habitat avoidance and habitat selection. Grey lines depict habitat types that covered a maximum of 20 % of the home range and for which extrapolation over the entire range may therefore be hazardous. Confidence intervals have been omitted to avoid overfilling of the graph.

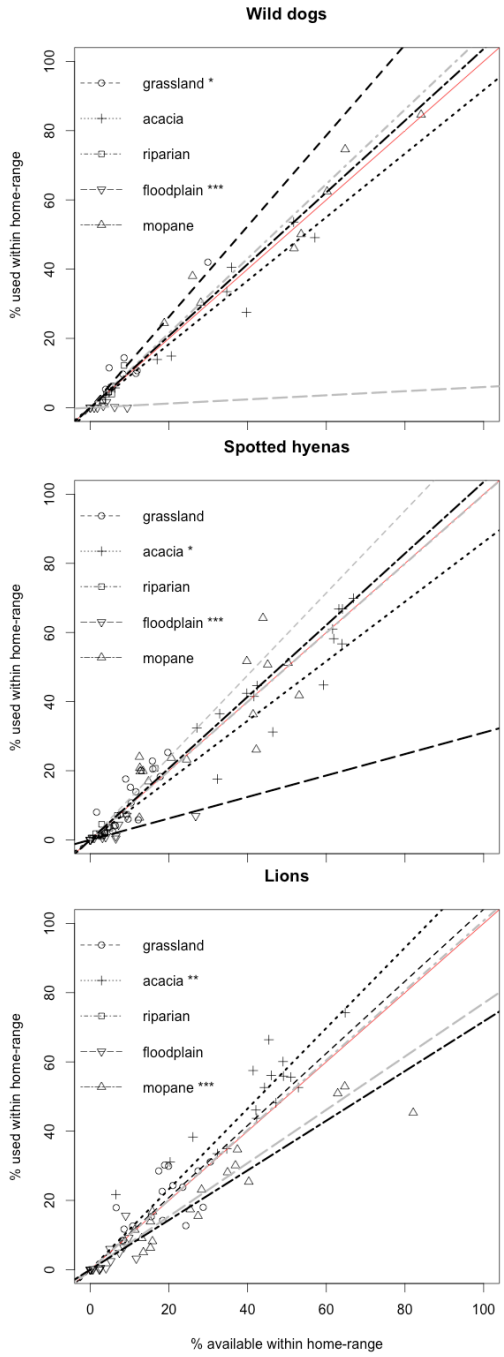


Figure 5: Likelihood of encountering lions, spotted hyenas and neighboring packs of wild dogs within discrete isopleths of the territory of the Mathew's pack. Pixel Values have been standardized around 0 by $y_{standardized} = y - mean(y)/stdv(y)$ to be representable on the same graph. Note that because same pixel values for lions and hyenas do not have the same significance (see text), between-species comparison is not permitted.

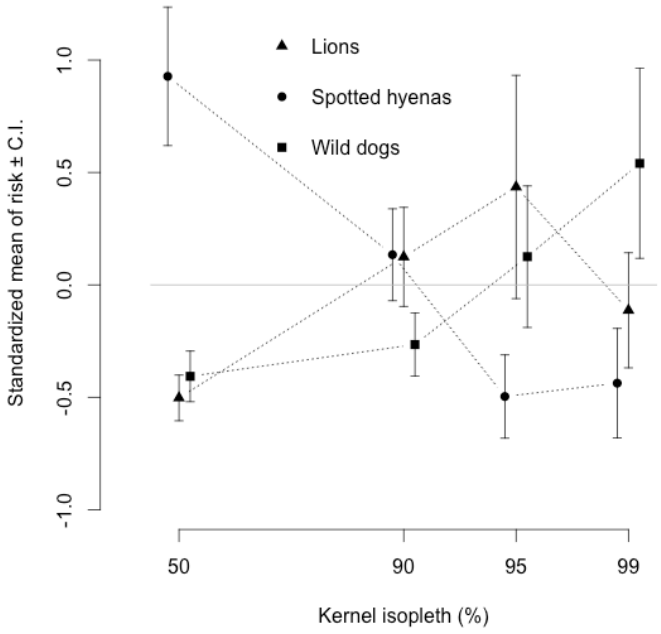
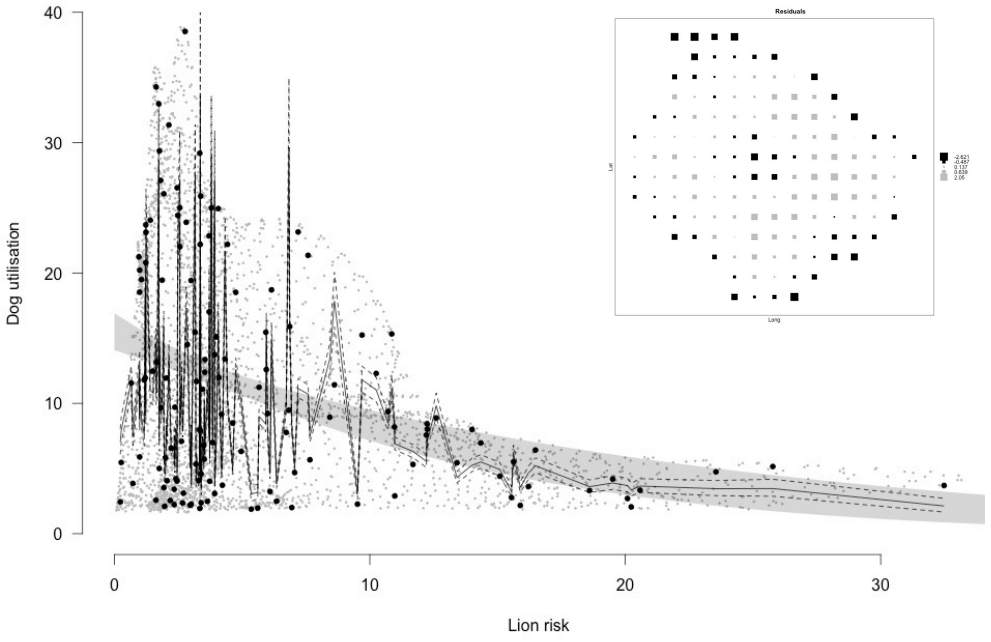


Figure 6: Likelihood of encountering wild dogs of the Mathew's pack in relation to the likelihood of encountering lions. Small grey dots represent all data and larger black dots represent the data (N = 198) extracted for analysis. Solid lines represent the model fitted values and dotted line the 95 % C.I. The grey area represent the 95 % C.I of a non-linear relationship of the form dogs ~ a * exp (-b * lion). The spatial autocorrelation of the model residuals is shown on the top right of the panel. The black dots in the middle of the territory emphasize that not all spatial structure of the data could be captured through the predictor variables analyzed.



ONLINE SUPPORTING INFORMATION

Material and Methods

Vegetation description and creation of the vegetation map

We categorized the different habitat types of the Okavango Delta into five major vegetation classes (Fig. 2A and Fig. S1): 1) floodplains, which comprised rivers, swamps, perennial floodplains and characterized by the presence of *Cyperus, papyrus, Schoenoplectus corymbosus and Imperata cylindrical*; 2) grass, which comprised seasonal and ephemeral floodplains and short grass savannah and characterized by the absence of trees and shrubs and by the presence of *Urochloa trichopus, Cynodon dactylon, Eragrostis rigidior* and other short-stem grass spp.; 3) mixed acacia, which comprised acacia savannah and denser acacia mixed woodland and characterized by the presence of evergreen *Acacia mellifera and A. erioloba* dispersed at variable densities in grasslands dominated by tall-stem grass species such as *Panicum maximum, Digitaria eriantha* and *Actyloctenium gigantium*; 4) riparian, which was characterized by riverine vegetation growing on elevated ground along extant or ancient channels and floodplains, and comprising *Hyphaena petersiana, Lonchocarpus capassa, Ficus sycomorus, Kigelia Africana, Croton megalobotrys, Combretum imberbe* and *Aacacia nigrescens*; and 5) mopane woodland, which was characterized by the almost exclusive presence of *Colophospermum mopane* growing on alkaline substrate (vertisol or black cotton soil) at different densities and heights (for a more detailed description of vegetation types see Bennit 2012).

We created a digital map of the five vegetation classes (Fig. 2A and Fig. S1) on the basis of SPOT satellite images (taken in October 2009) with a 30 x 30 m (= one pixel) resolution. In a first step, open water features (vegetation class 1), characterized by a very low reflectance in the near-infrared spectrum, were delineated. To differentiate the other four vegetation classes, 40 locations were selected within each habitat type and an area of the corresponding vegetation type delineated around each location. Half of the so created areas were used to train the software (ENVI 4.8) in the categorization of the vegetation classes and the other half

for proofing the accuracy of the classification. Reflectance differences between vegetation types in the Red, Green, Blue (RGB) and in the Near-InfraRed (NIR) spectrum as well as the Normalized Differenced Vegetation Index (NDVI) were used to differentiate vegetation classes. After all procedures and corrections, accuracy for the all study areas was 72.4%.

Habitat structure, visibility

Based on morphological and structural characteristics, each of the four classes: grass, mixed acacia, riparian and mopane was further subdivided in two subclasses. Subclasses were characterized by the same grass and tree species compositions, and therefore showed the same spectral reflectance and were not separable following the above-mentioned protocol, but presented substantial differences in their physical and spatial organization.

We defined visibility as the distance at which a 60 x 60 cm brown cardboard sheet attached to a pole at 80 cm from the ground (thus mimicking the size of a wild dog or a stalking lion) was not visible to an observer crouched at 1 m above ground. To calculate visibility, 20 locations within each subclass were sampled four times during 2010, in the middle and at the end of the wet and dry season (January and April, respectively, July and October). At each of the sampled locations, the observer (G. Cozzi or F. Broekhuis) walked away from the cardboard sheet until it completely disappeared to the sight, the same procedure was repeated in the four cardinal directions and the four values averaged. For safety reasons, the measurement was interrupted upon reaching a distance of 200 m from the cardboard (and vehicle). The distance between the observer and the cardboard was measured using a Garmin EtreX Legend with an accuracy of ± 4 m. Because of inaccessibility, no locations on floodplains were sampled and visibility was assumed to equal or exceed visibility in grassland. Because substantially different visibility scores characterized vegetation subclasses but levelled out at the class level, visibility scores could not be used in further analyses linking visibility to vegetation classes (Fig. S2).

Figure S1: Vegetation types and NDVI values for the entire study area spannign over approximately 4'000 km^2. For a detailed description of the color codes see Figure 2 in the main text.

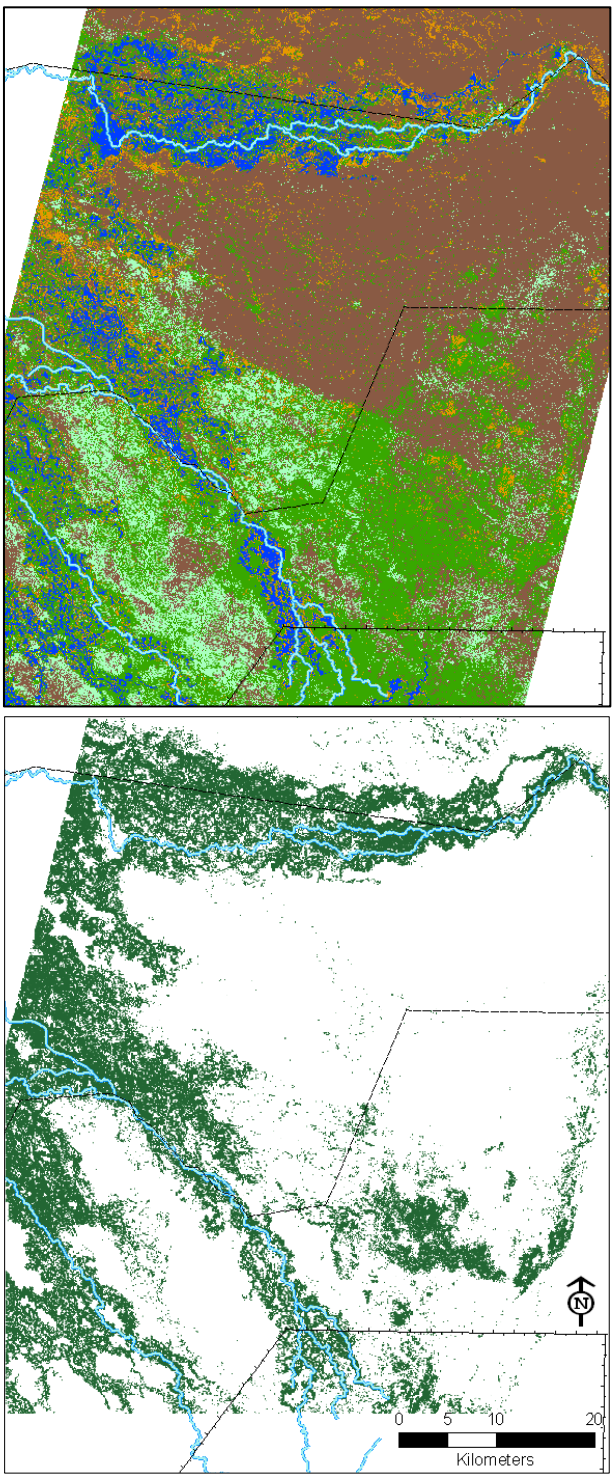


Fig S2: Boxplot showing visibility scores for different vegetation subclasses and classes during the dry and wet season. Based on satellite imagery analysis (see text) subclasses were merged into four classes: Acacia = Acacia mixed woodland (Amw), Acacia shrubs (As) and Acacia savannah (Asav); Grass = grass-dominated grassland (Gg) and sage-dominated grassland (Gs); Mopane = mopane shrubs (Ms) and tall mopane forest (Mt); Riparian. A slightly overall increased visibility during the dry season when vegetation was senescent could be observed. Because of the significant differences within subclasses belonging to a class (depicted by the non-overlapping notches and visually roughly categorized by horizontal dashed lines) and the small differences between classes, visibility scores were not used for further analyses.

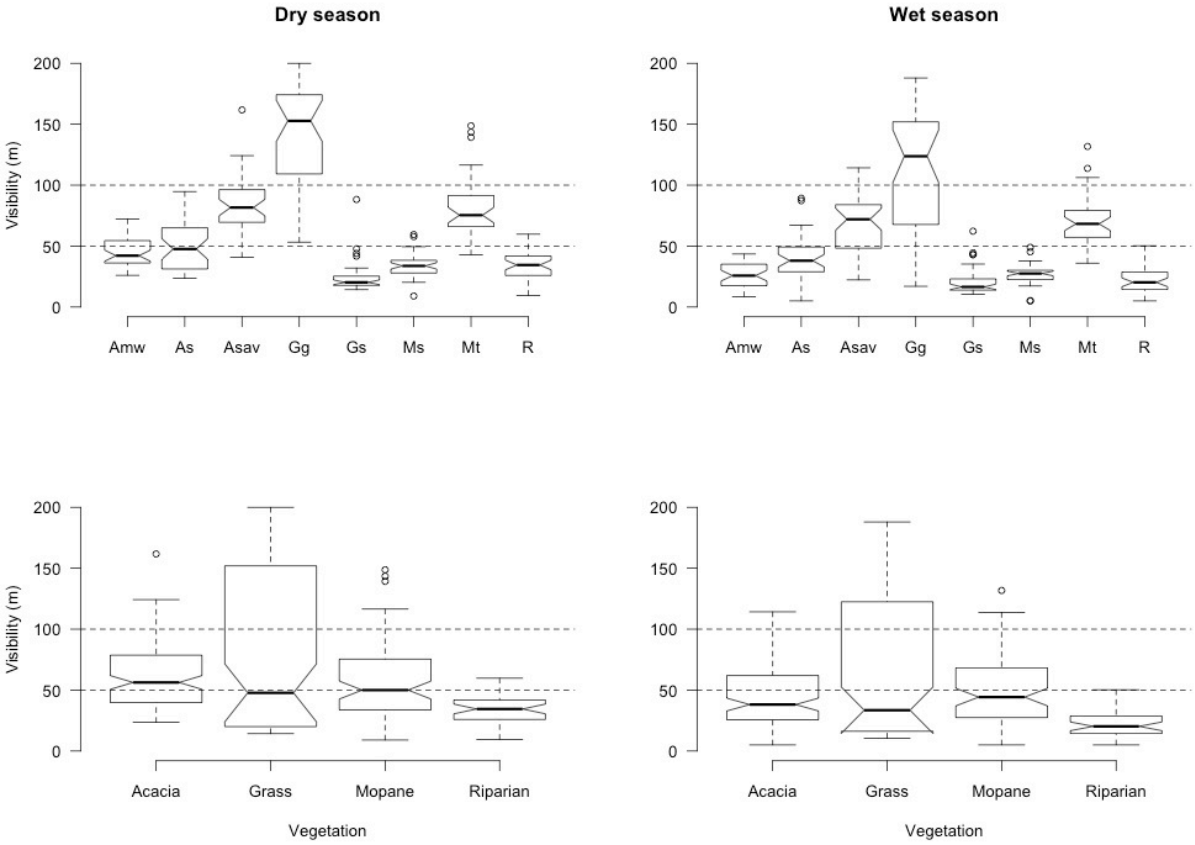
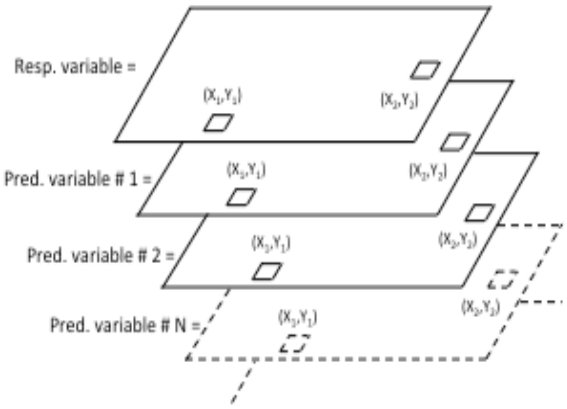


Figure S3: Conceptual flow-chart of the analytical spatial approach. Within each layer (response or predictor variable) a value is assigned to each pixel centred around X_n,Y_n Cartesian coordinates. The response variable and explanatory variables are thus spatially associated to each other by means of their geographic location.



Chapter Four

Comparison of the effects of artificial and natural barriers on large African carnivores: Implications for inter-specific relationships and connectivity.

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Top: A young male lion is resting near the buffalo fence, a non electrified fence that, despite erected to constrain the movements of buffalos, negatively effects movements and space use of lions (photo courtesy Krystyna Jordan).

Bottom: A group of African wild dogs hesitates in the vicinity of a water Channel. Water bodies represent a hard boundary for wild dogs that, like spotted hyenas and cheetahs, only very rarely cross them.

Comparison of the effects of artificial and natural barriers on large African carnivores: Implications for inter-specific relationships and connectivity

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Running Headline: Influence of barriers on large carnivores

SUMMARY

1. Physical barriers contribute to habitat fragmentation, influence species distribution and ranging behaviour, and impact long-term population viability. Barrier permeability varies among species and can potentially impact the competitive balance within animal communities by differentially affecting co-occurring species. The influence of barriers on the spatial distribution of species within whole communities has nonetheless received little attention.

2. During a 4 year period, we studied the influence of a fence and rivers, two landscape features that potentially act as barriers on space use and ranging behaviour of lions *Panthera leo*, spotted hyenas *Crocuta crocuta*, African wild dogs *Lycaon pictus* and cheetahs *Acinonyx jubatus* in Northern Botswana. We compared the tendencies of these species to cross the barriers using data generated from GPS-radio collars fitted to a total of 35 individuals. Barrier permeability was inferred by calculating the number of times animals crossed a barrier vs. the number of times they did not cross. Finally, based on our results, we produced a map of connectivity for the broader landscape system.

3. Permeability varied significantly between fence and rivers and among species. The fence represented an obstacle for lions (permeability = 7.2%), while it was considerably more permeable for hyenas (35.6%) and wild dogs and cheetahs (≥ 50%). In contrast, the rivers and associated floodplains were relatively permeable to lions (14.4%) while they represented a nearly impassable obstacle for the other species (< 2%).

4. The aversion of lions to cross the fence resulted in a relatively lion-free habitat patch on one side of the fence, which might provide a potential refuge for other species. For instance, the competitively inferior wild dogs used this refuge significantly more intensively than the side of the fence with a high presence of lions.

5. We showed that the influence of a barrier on the distribution of animals could potentially result in a broad-scale modification of community structure and ecology within

a guild of co-occurring species. As habitat fragmentation increases, understanding the impact of barriers on species distributions is thus essential for the implementation of landscape-scale management strategies, the development and maintenance of corridors and the enhancement of connectivity.

Keywords: animal behaviour; coexistence; large carnivore guild; movement pattern; spatial distribution; spatial refuge; sympatric species

INTRODUCTION

Large-scale landscape features such as natural and artificial barriers contribute to habitat fragmentation and limit connectivity and can thus impact animal communities and threaten the long-term viability of species (McDonald & St. Clair 2004; Cozzi, Müller & Krauss 2008; Fahrig & Rytwinski 2009; Morales et al. 2010). Barriers have for instance been shown to alter ranging behaviour, dispersal, gene flow and distribution of a broad range of species (e.g. Shepard et al. 2008; Fahrig & Rytwinski 2009 and references therein, Tracey et al. in press). When species co-occur in a landscape system, differential effects of barriers may change the spatial distribution and overlap of species and thus community structure (Didham et al. 1996).

To date, however, the majority of the studies investigating the impact of barriers on free-ranging animals have focused on a single species (e.g. Trombulak & Frissell 2000 and examples therein; Dodd et al. 2007; Vanak, Thaker & Slotow 2010) rather than on entire communities or groups of species and their interactions. For example, Blanco et al. (2005) showed that a river constrained the range expansion of wolves *Canis lupus* in Spain, yet they did not examine the consequences of the changed spatial distribution of wolves on other competing predator species. Only a few studies have described the extent to which barriers might influence the spatial distribution of species within guilds or whole animal

communities (St. Clair 2003, McDonald & St. Clair 2004). If barriers affect species differentially, we would expect barriers to influence the spatial distribution and interactions among co-occurring species (Frantz et al. 2012). For example, the exclusion of a species incapable of crossing a barrier may release other species from competition and predation. Medium-sized predators are, for instance, believed to benefit from the removal of larger predators in mammalian carnivore guilds (Crooks & Soule 1999; Berger, Gese & Berger 2008).

The permeability of a barrier to animal movements mainly depends on the animal's perception, its needs and motivation to cross, and ultimately on the physical characteristics of both animals and barriers (Wiens, Crawford & Gosz 1985; McDonald & St. Clair 2004; Lagendijk et al. 2011; Frantz et al. 2012). Therefore, barriers will often limit connectivity among habitat patches and may intensify or reduce interactions among co-occurring species restricted within progressively smaller and more isolated habitat patches. For integrative species conservation management, barriers represent a particular concern and challenge because their effects on animal populations and community structure are difficult to predict (Bélisle & St. Clair 2001; Lagendijk et al. 2011; Slotow 2012). Thus, understanding the impacts of artificial and natural barriers on the ranging behaviour of animal species is essential to ensure connectivity among populations and for the successful implementation of conservation strategies for endangered species (e.g. Kaczensky et al. 2011; Zeller, McGarigal & Whiteley 2012; Tracey et al. in press).

In this paper we compared the influence of fences and rivers, two potential barriers, on large carnivores in the Okavango Delta in Botswana as a case study. In this region, the negative effects of fences have already been documented for wild ungulate species (Mbaiwa & Mbaiwa 2006; Bartlam-Brooks, Bonyongo & Harris 2011) but nothing is known about the effects of fences on space use and ranging patterns of large carnivores. The Okavango Delta is part of the five nations Kavango-Zambezi Rivers ecosystem

(KAZA) transfrontier project and understanding the impact of barriers on species distributions is essential for the implementation of management strategies for an international project that aims at creating a protected area for wildlife across Africa.

In particular, we investigated the effects of one fence and three rivers on four co-occurring large carnivore species, the lion (*Panthera leo* Linnaeus), the spotted hyena (*Crocuta crocuta* Erxleben), the African wild dog (*Lycaon pictus* Temminck) and the cheetah (*Acinonyx jubatus* Schreber). Data were generated from GPS-radio collars fitted on a total of 35 individuals. We analysed, for each species, its use of space on both sides of the barriers, assessed barrier permeability and explored the spatio-temporal characteristics of crossing locations. We further investigated whether low barrier permeability resulted in reduced presence of competitively superior predator species in particular habitat patches that might be used more intensively by competitively inferior species. Finally, we used our results to develop a map of habitat connectivity for the broader landscape system.

MATERIAL AND METHODS

Study area

This study was carried out between 2007 and 2011 in the Okavango Delta, a wildlife-managed landscape system of roughly 20,000 km^2 in Northern Botswana. As explained below, the study area (centred at: S 19.523°; E 23.635°) included a 60 km section of a government constructed and maintained veterinary fence and three branches of the Okavango River (Fig. 1A).

The Southern Buffalo Fence

The Southern Buffalo Fence (hereafter referred to as the 'fence') is a 225 km veterinary fence that surrounds the perennial waters of the Okavango Delta. It was erected in 1983 with the main purpose of separating Cape buffalos (*Syncerus caffer* Sparrman) from cattle

to hinder the transmission of foot-and-mouth disease. The fence is not electrified, is 1.6 m high and is composed of eight parallel smooth wires spaced at 20 cm intervals.

The northern side of the fence (hereafter referred to as the 'wildlife side') includes Moremi Game Reserve and the surrounding Wildlife Management Areas (Fig. 1A). In this area, photographic tourism and trophy hunting are the only permitted human activities. All major prey species of lion, spotted hyena, African wild dog and cheetah, such as Cape buffalo, zebra (*Equus burchelli)*, kudu (*Tragelaphus strepsiceros)*, impala (*Aepyceros melampus)*, warthog (*Phacochoerus aethiopicus)* and steenbok (*Raphicerus campestris)* (e.g. Hayward & Kerley 2008), are common on the wildlife side of the fence (G. Cozzi, unpubl. data).

The southern side of the fence (hereafter referred to as the 'livestock side') is dominated by cattle farms practicing subsistence pastoralism. A total of 36 farms are situated within 10 km of the fence; the mean number of livestock animals per farm is 47 (min. 5; max. 164) (data from Sebogiso et al., in prep.). Natural prey species have been recorded on the livestock side but their occurrence is rare (G. Cozzi, pers. obs.). Predator species may compensate for the limited abundance of natural prey on the livestock side by preying upon livestock. Among the four species investigated here, spotted hyenas were reported causing the majority of the losses, while the other species predated livestock less frequently (Gusset et al. 2009, O. Sebogiso pers. comm.). Because tolerance of predators depends on the extent of predation, and because the Botswana government does not compensate livestock losses to hyenas, farmers are particularly intolerant towards this species (O. Sebogiso pers. comm.).

Rivers

Three branches of the Okavango River cross the study area: the Gomoti, the Santantadibe and the Khwai Rivers (Fig. 1A). In the study area, the amount of water and the through-

flow in the three rivers (they variably terminate in the Kalahari sands of northern Botswana) typically peak in July and subside rapidly reaching the lowest level early in the year. Overall, water levels in the rivers consistently increased between 2007 and 2011 due to exceptional rains. The sections of the three rivers within the study area never dried out during the study period, while the rivers occasionally dried at their distal terminus.

Field work and data collection

We systematically recorded location data of individual lions, spotted hyenas, African wild dogs and cheetahs using programmed GPS radio-collars (Vectronic Aerospace GmbH, Germany). As required by law, target animals were immobilized for collaring purposes by a qualified wildlife veterinarian using approved techniques and drug combinations (Osofsky, McNutt & Hirsch1996, Kock, Meltzer & Burroughs 2006). All captures took place north of the fence and east of the Gomoti River (with the exception of a dog resident in a pack on the western side). The data presented here are from fourteen lions in six prides, ten spotted hyenas in six clans, six African wild dogs in four packs and five individual cheetahs (Fig. S1–S4 in Supporting Information).

The collars were scheduled to record several GPS locations per day. For lions and hyenas, one location was recorded every two hours between 18:00 and 06:00 and one location was recorded at noon, giving a total of eight GPS locations per day. For wild dogs, GPS locations were recorded at 06:00, 12:00 and 18:00, and for cheetahs at 06:00, 12:00, 18:00 and 24:00. On average, collars successfully recorded 84.8 ± 3.20% (mean ± s.e.m) of the scheduled locations. In a test, 14 randomly selected collars were placed at known GPS locations under thick canopy cover and the distance between each GPS location collected by the collars and their actual location was measured in ArcGIS 9.2 (ESRI, United States). The GPS locations (n = 246) collected by the test collars were used to

predict their accuracy, which was 11.62 m ± 4.05 m (mean ± s.e.m), and was assumed to be representative for the accuracy of all collars deployed in the field.

Use of space

To investigate space use in the vicinity of a barrier we analysed for each individual and species the distribution of all GPS locations within 5 km on either side of each barrier. This measure was chosen to be larger than the average distance between two consecutive GPS locations moved by wild dogs, the most mobile of the four species, which was 3.53 ± 0.15 km (mean ± s.e.m.), and thus considered adequate to capture important ecological processes. We limited our analysis to the locations in the vicinity of the barriers because we had insufficient information about additional covariables (i.e. in addition to distance from the barrier), which might affect the animals' distributions further away from the barriers. We expected that if a barrier did not influence the use of space we would not observe a significant difference in the distribution of GPS locations on either side of the barrier; instead we would only observe a gradual decrease in the number of GPS locations the further away an animal is from the core of its territory. In contrast, an abrupt change in the number of GPS locations between the two sides of a barrier would suggest an effect of the barrier on an animals' use of space. Because the spatio-temporal autocorrelation structure of the data gives information about an animal's perception of the surrounding landscape, we did not subsample from the location time series of individual animals and instead retained all data within 5 km on either side of the barriers (Legendre 1993; Willems & Hill 2009).

Within this 5 km range, locations were binned to investigate the relationship between the number of locations and the distance to the barrier. We defined 100 m wide bins and we then calculated, for each species and barrier type, the average number of GPS locations within each bin (because not all individuals were recorded within each bin,

averages allowed avoiding zero-inflation-related issues). Bin width was chosen to avoid excessive binning, yet without smoothing actual displacements, (for example, resting animals may move a few tens of meters to keep in the shade; G. Cozzi pers. obs.). The average number of GPS locations in each bin was used as the response variable in a polynomial model with distance from the barrier and its square (distance^2 = area), barrier side (N and S for the fence and W and E for the rivers) and interaction between distance and barrier side as predictor variables. The response variable was log-transformed to meet the assumption of normality of residuals. Clusters of GPS locations known to correspond to den sites or large carcasses (i.e. elephants *Loxodonta africana* Blumenbach and giraffes *Giraffa camelopardalis* Linnaeus) were treated as outliers and, unless specified, removed from the models. For all statistical analyses, model simplification startied from a full model and followed a backward selection procedure based on the Akaike Information Criterion (Zuur et al. 2009).

Crossing likelihood and movement metrics

We investigated the likelihood of crossing a barrier by calculating the number of times animals crossed a barrier vs. the number of times they had the potential to cross a barrier but did not. For each individual, we created a continuous movement path by connecting consecutive GPS locations using Hawth's Tools for ArcGIS 9.2 (Beyer 2004). The segment between two consecutive GPS locations is hereafter referred to as a 'step'. Steps that had at least a portion of their length within a distance from the barrier equal to half the average step length (specific to each individual) were considered as potential crossing events. To each one of these potential crossing events, we assigned a value of '1' if the animal crossed a barrier and a value of '0' if the animal did not. Because the criterion of half the average step length is somewhat arbitrary, we repeated the analysis considering all steps within a distance equal to the full average step length. The qualitative outcome

remained unchanged and we therefore present only the results derived from data selected using the criterion of half the average step length. We analysed crossing likelihood using a generalized linear mixed-effects model (GLMM) with binomial distribution and accounted for over-dispersion of the data. Steps (crossing vs. non crossing) were entered as binary response variable; barrier type (i.e. fence or river) animal species and year (as a proxy for the increasing water level) were entered as fixed effects; animal identity was entered as random effect.

To further investigate the influence of a barrier on animal movement patterns, we investigated net displacement between four consecutive steps (i.e. the distance between the beginning of $step_i$ and the end of $step_{i+4}$) in the vicinity of the barriers (i.e. within a distance of half the average step length) and at random locations away from the barriers. Furthermore, we analysed the directionality of the steps in the vicinity of the fence (the same analysis was not done for the rivers due to their tortuosity). To each step we assigned a bearing between 0° and 90°. A step of 0° thus represented a movement perpendicular to the barrier and a step of 90° a step parallel to the barrier (no distinction was made if an individual was moving eastward: 90°, or westward: 270°). The necessary corrections were made for the diagonal (western) and vertical (eastern) section of the fence (see Fig. 1A). Steps shorter than 50 m were not considered because they were more likely to represent a stationary than a movement event. The bearing of each step was entered in a mixed-effects model with species as fixed explanatory term and individual as random term. Because angles were bound between 0° and 90°, we used the following transformation to meet assumptions of normality: $y = \sin^{-1}\sqrt{A}$; where: $A = angle/(\frac{\pi}{2})$. Species showing a predicted bearing smaller than 45° were consequently considered to mainly move to and from or across the fence, species showing an angle larger than 45° were considered as mainly moving along the fence.

RESULTS

Not all individuals had contact with both barriers (defined as recording at least one GPS location within 100 m from a barrier). Nine lions had contact with the fence but only four were recorded on both sides. The same applied to seven of nine spotted hyenas, all wild dogs and one of two cheetahs. Thirteen lions ad contact with the river and nine of them were recorded on both sides. Similarly, one of six spotted hyenas, one of four wild dogs and three of five cheetahs were recorded on both sides. Individuals reached the other side of a barrier in different ways. Our GPS records indicated, for example, that one hyena, one wild dog and one cheetah travelled around the drying terminus of the Gomoti River on several occasions rather than crossing it (see below and Fig. 1B), while lions crossed the river and inundated floodplains directly.

Use of space

We observed a significant decrease in the number of lion GPS locations from the wildlife side to the livestock side of the fence (distance by side interaction term: $F_{1,95} = 13.99$, $p <$ 0,001) (Table S1 & Fig. 2A & 2C). In contrast, spotted hyenas, wild dogs and cheetahs were not negatively influenced by the fence, and instead showed a steady decrease in the number of GPS locations with increasing distance from the core area of their territory (i.e. moving from north to south) (Table S1 & Fig. 2A & 2C). Wild dogs even showed a marginally significant increase in the number of locations on the livestock side of the fence ($F_{1,96} = 2.81$, $p = 0.097$). This figure was highly significant ($F_{1,96} = 10.67$, $p = 0.002$) when we retained in the analysis locations around the den site (Table S1 & Fig. 2A).

For all four species, there was a significant difference in space use (i.e. number of GPS locations) between opposite sides of the rivers (polynomial distance by side interaction term: lions: $F_{2,94} = 24.76$, $p < 0.001$; spotted hyenas: $F_{2,94} = 20.01$, $p < 0.001$; wild dogs: $F_{2,94} = 15.80$, $p < 0.001$; cheetahs: $F_{2,94} = 32.84$, $p < 0.001$) (Table S1 & Fig. 2B

&2C). For hyenas, cheetahs and wild dogs this difference represented an almost complete lack of locations on the western side of the river, while for lions this difference resulted from the evident decrease of locations in the immediate vicinity of the western side of the river (cf. Fig. 2B, lion panel).

Crossing likelihood and movement metrics

Our results showed a significant difference among species in the crossing likelihood (interaction term barrier by species: $F_{3,20} = 87.69$, $p < 0.001$). In general, the response of lions was the inverse of the other species (Fig. 3A). Lions had a fence-crossing likelihood equal to 3.6% meaning that they crossed the fence 3.6 times for every 100 'steps' they made in its vicinity. In contrast, spotted hyenas, cheetahs and wild dogs had fence-crossing likelihoods of 17.8%, 25.5% and 30.7%, respectively. In contrast, water bodies were almost impermeable to spotted hyenas, wild dogs and cheetahs while they were considerably more permeable for lions (Fig. 3A). The river-crossing likelihood for lions was 7.2%, and was one to two orders of magnitude higher than the permeability for cheetahs, wild dogs and spotted hyenas, which were, respectively, 0.8%, 0.6% and 0.1%. We could furthermore detect a significant negative trend in river-crossing likelihood across years ($F_{4,1693} = 11.2$, $p < 0.001$), with 2007, the driest year, being characterized by the highest crossing likelihood (Fig. 3B).

Because, under an assumption of random movement, half the number of steps in the vicinity of a barrier are expected to end in the animal crossing and the other half in the animal not crossing a 50% crossing likelihood is equal to a 100% barrier permeability. If we correct for this factor, fence permeability for the smaller wild dog and cheetah was higher than 50%, for the medium-sized spotted hyena was 35.6 % and for the larger lion was only 7.2%. River permeability was 14.4% for lions and less than 2% for the other three smaller species.

We found that species net displacement varied significantly depending on the animals' location, i.e. in the vicinity of the fence, in the vicinity of the rivers, or further away from any barrier ($F_{6,3908} = 6.68$, $p < 0.001$). In particular, within species, lion and cheetah displacement near the rivers was considerably shorter than at random locations away from any barrier. Hyena net displacement was, instead, considerably shorter in the vicinity of the fence. We did not detect any significant differences for wild dogs (Fig. 3C). Note that because of differences in the collection of GPS data (see Methods), direct comparison across species is only possible between lions and hyenas. The movements in the vicinity of the fence were also significantly different between the four species ($F_{1,3} = 12.44$, $p < 0.001$). In particular lions, which tended to move along the fence, differed considerably from hyenas and wild dogs both of which tended to move more perpendicularly to it (Fig. 3D). Cheetah movements could not be classified in this way because only two cheetahs had contact with the fence; one crossed while the other never did.

Characteristics of crossing locations

Given the relatively small number of fence crossing events for lions (n = 24), crossing points were visually investigated. On ten occasions (41.7%), lions crossed the fence in the immediate vicinity of the floodplains associated with the Gomoti and Santantadibe Rivers where the fence had been observed to be in very poor conditions (see Hydrology section in Supporting Information). All ten crossing events occurred during 2007 and 2008, between mid September and mid November, a period that coincided with a low water level; no crossing events along floodplains were recorded during 2009–2011. No distinct characteristics were found for the other 14 crossing points. Spotted hyenas (n = 732 crossings), wild dogs (n = 145 crossings) and cheetahs (n = 16 crossings) crossed at any point along the entire length of the fence. Similarly, lions crossed at any point along the

course of the rivers. After we corrected for the number of locations within each month, crossing frequency peaked towards the end of a calendar year, the time when water levels were lowest. Crossing frequency for lions was highest during 2007 and lowest during 2011. The only hyena that crossed the river did so three times within 24 hours at what appears to be one single crossing point. The same hyena circumvented the Gomoti on three occasions between December 2007 and January 2008. Similarly, the only wild dog that was recorded on both sides of the Gomoti circumvented it three times and crossed it once in February 2009. Evidence suggests that the crossing location corresponded to the only location known to the authors for crossing by car along an exposed sand bank. One cheetah circumvented the Gomoti during August and September 2010 (high water level) but never crossed it, while two other cheetahs crossed the river on three occasions.

DISCUSSION

Investigating the distribution and ranging behaviour of animal species in relation to various types of artificial and natural barriers is fundamental to assessing their aptitude for traversing obstacles, understanding the spatial relationships between co-occurring species, and to managing connectivity between suitable habitat patches (Didham et al. 1996; McDonald & St. Clair 2004; Blanco, Cortés & Virgós 2005; Kaczensky et al. 2011; Zeller, McGarigal & Whiteley 2012). Our results based on simultaneous observations of four species of the African large predator guild in northern Botswana demonstrate that the permeability of a barrier can vary considerably among taxonomically related species. We showed that lions were strongly restricted by a not-electrified eight-strand smooth wire veterinary fence built to control the movements of ungulate species. The same fence had no obvious effect on the ranging behaviour of the smaller spotted hyenas, wild dogs and cheetahs. It should be noted, however, that the results of the influence of the fence on cheetahs are based on only two individuals (one which crossed and which did not).

Nevertheless, a similar limited effect of cattle fences can be anticipated for Namibia, where the majority of cheetahs live and moves on farmlands subdivided by fences similar to the one in our study area. In contrast to the effects of fences, lions regularly crossed rivers and associated floodplains, while the same expanses of water constituted comparatively impermeable barriers to the three other species (see Hydrology section in Supporting Information for a further discussion). The physical characteristics of a barrier and species-specific behaviours (cf. Fig. 3C & 3D) thus appear to be important characteristics in determining the permeability of a barrier (Wiens, Crawford & Gosz 1985; Clevenger & Waltho 2000, Kerth & Melber 2009). Substantial structural differences between barrier types may further influence an animal's perception resulting in differential likelihood of crossing.

Our findings emphasise that because barrier permeability varies among the members of a community, barriers can influence the spatial distribution and relationship of otherwise co-occurring species by excluding some species but not others from particular habitat patches, thus affecting community structure. Exclusion of competitively dominant species may trigger a succession of downward cascade events that influence community assembly (Lagendijk et al. 2011, Slotow 2012). This shows the importance of a multi-species approach where functionally sympatric groups of animals are considered simultaneously. A possible explanation of the observed ranging behaviour of the competitively inferior species (i.e wild dogs and cheetahs) on the livestock side of the fence could suggests that these may benefit from competition and predation release due to a lower lion presence. Predation by lions is a major cause of natural mortality in adult and juvenile wild dogs, particularly during the denning period (Mills & Gorman 1997). This antagonistic relation might explain the increased presence of wild dogs on the livestock side of the fence during times of the year when they were denning (Fig. 2A). This hypothesis is in line with a study by van der Meer et al. (2011) who concluded that a

higher risk and cost of kleptoparasitism inside Hwange National Park might have contributed to habitat choice of African wild dogs outside the park. The GPS data from our study showed that the wild dogs, which denned south of the fence (data not shown) daily returned to the wildlife side instead of hunting on the livestock side, thus weakening the alternative hypothesis that the presence of wild dogs south of the fence was due to an easily accessible prey base (small stock). These interspecific dynamics are also consistent with findings from Namibia where cheetahs are reported to thrive on farmland due to the low density of lions outside protected areas (Marker-Kraus 1996). No such pattern was detected for cheetahs in our study, possibly due to the small sample size.

Following the proposed competition exclusion hypothesis, the fence may in effect encourage species that seek spatial refuge from superior competitors to move closer to human activities where they eventually suffer direct persecution (Balme, Huner & Slotow 2010; van der Meer et al. 2011). This may finally function as an ecological trap where the high mortality rate outside protected areas can have negative consequences on protected populations (Balme, Hunter & Slotow 2010). This possible scenario should be carefully taken into consideration for the conservation of species such as the African wild dog and the cheetah that are listed as endangered and vulnerable, respectively, according to the International Union for Conservation of Nature (IUCN). We nonetheless acknowledge that other confounding variables, such as species-specific habitat suitability or small-scale prey distribution, may influence the observed patterns. We therefore encourage that these alternative hypotheses be explored in the future.

In contrast to our observations, lions have been reported to frequently cross (electrified) fences in several other parts of Africa. The main reason for this permeability has been attributed to a lack of maintenance and the poor conditions of the fences (Stander 1990, Funston 2001, Hemson 2003). The well-maintained nature of the Southern Buffalo Fence may thus have been a major cause for the pattern observed in this study. Our

conclusion is supported by the fact that in 41.7% of the observed crossing events, lions crossed near sections of the fence destroyed by water (see Hydrology section in Supporting Information). Because the utility of a fence is related to the costs of building and maintenance it and its effectiveness in controlling animal movements (e.g. Vercauteren, Lavelle & Hygnstrom 2006; Slotow 2012), our findings have economic implications. More research on this topic would be necessary for a full cost-benefit analysis. A low but well-maintained fence might thus be more effective in controlling lion movements than an electrified but damaged fence. The low presence of lions on the livestock side of the fence in our study was additionally supported by an extensive questionnaire survey (O. Sebogiso pers. comm.) and by spoor surveys carried out during this study (data not shown). Also consistent with these observations, farmers in the area adjacent to our study populations reported that livestock losses from lions were lower than losses from spotted hyenas (Gusset et al. 2009). Despite being erected for other purposes, the fence thus proved effective in reducing human-wildlife conflict with lions, which could be further improved with more consistent maintenance. We encourage further investigation to explore the potential of cattle fences to protect livestock or villages. Alternatively, a lack of motivation to cross, possibly due to the high abundance of prey species on the wildlife side, may also have influenced the lions' distribution across the fence.

The negative relationship between crossing likelihood and water levels across years (Fig. 3B) shows how the changing hydrology of the Okavango influences movements across rivers. The Okavango is an extremely dynamic system historically characterized by conspicuous, natural hydrological fluctuations. Our work, however, anticipates how changes in water levels, which in the coming years are likely to increase under the influence of climate change (e.g. Aldous et al. 2011), could change the dynamics of other inland systems that are historically more stable. This case study represents an additional example of the need to incorporate the effects of changing hydrology, and more in general

climate change, on the management policies of protected areas (e.g. Hannah 2010; Groves et al. 2012).

The obstacles represented by the fence and the rivers have major consequences for habitat connectivity in the Okavango Delta. The rivers that run north–south represented a barrier to the west–east movements of spotted hyenas, wild dogs and cheetahs and to a lesser extent of lions. During wet years (e.g. this study), when all rivers flow past the fence, connectivity between habitat patches may be almost entirely granted by individuals travelling around the drying terminus of the rivers through the hostile farming area south of the fence (Fig. 1). During periods of droughts, however, when water levels are lower and river permeability increases (Fig. 3B), connectivity may be granted north of the fence by movements across the rivers or across dry sections of the rivers. It is beyond the scope of this paper to exactly quantify connectivity between habitat patches; however, it seems that the southern region of the Delta, where human activities concentrate, is essential in maintaining habitat connectivity within and across the broad landscape system. Similarly, it has been shown that the effects of conservation schemes outside protected areas can positively influence conservation within such areas (Balme et al. 2009). We therefore encourage educational schemes, which enhance tolerance towards carnivores and protection of predator species through implementation of a wildlife–friendly law. This should be included in the larger concept of the KAZA transfrontier project for the Okavango ecosystem.

This study demonstrated that the permeability of different types of barriers can vary widely among species. Variable permeability can directly and indirectly (e.g. through reduced competition) affect the distribution of animal species and lead to shifts in community structure different abundances in habitat patches. The previously documented effects of barriers on the distribution, dispersal behaviour, social structure and gene flow of

species will thus also be combined with changes in species composition. These results emphasize the need for multi-species approaches in landscape-scale studies and planning.

AKNOWLEDGEMENTS

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FIGURES

Figure 1: The study area in the Okavango Delta, Northern Botswana and a qualitative representation of habitat connectivity for the species that easily cross the fence but not the rivers. The red circle (Panel A) highlights the two barrier types under investigation: a 60 km section of the Southern Buffalo Fence (brown, ticked line) and three effluents of the Okavango River, namely the Santantadibe, the Gomoti and the Khwai Rivers (from bottom to top and from left to right). Rivers and perennial floodplains are depicted in dark blue and light blue, respectively. Moremi Game Reserve is shown in green. During periods of high water levels, when rivers cross the fence, connectivity between the eastern and western side of the Delta, as well as between peninsulas may be almost only granted by individuals moving around the drying terminus of the rivers (black, dotted lines in Panel A, and enlarged section in Panel B) through, hostile, cattle farming areas (diagonal hatching). During periods of droughts, however, connectivity may be granted north of the fence by movements through dry sections of the rivers (see main text for more details). An enlarged section of the study area (Panel B) showing a 7 days and 53.5 km route of a group of wild dogs (solid purple line) and an 11 days and 54.2 km route of a cheetah (dashed orange line) that travelled around the drying terminus of the Gomoti River.

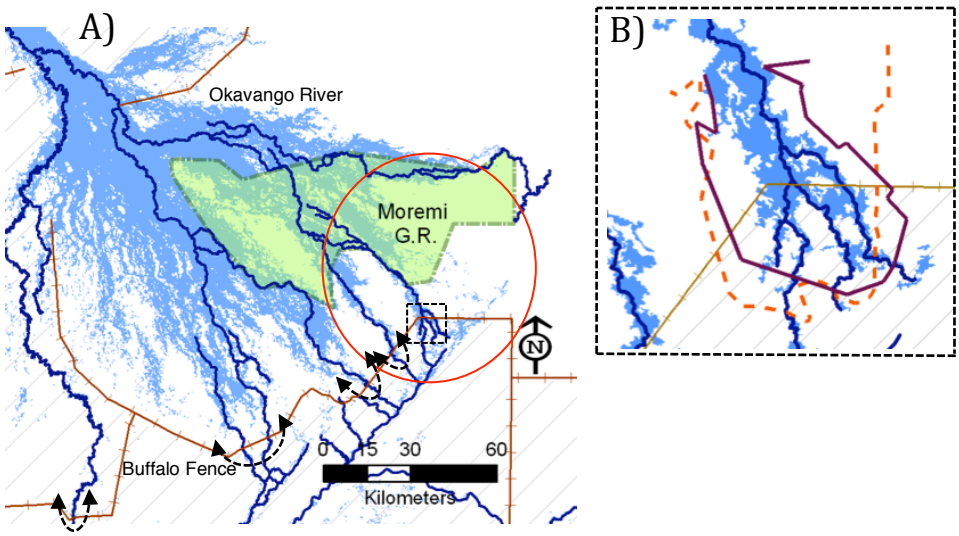


Figure 2: Mean number of GPS locations (open dots) on either side of A) the fence (Panel A) the rivers (Panel B) and a spatial representation of the real distribution of each individual of the four species (Panel C). The black solid lines represent model fitted values; the line through the middle of the graphs represent the barriers; the arrows represent an increased number of locations due to the presence of large carcasses and den sites (Panels A & B). These outliers were not retained in the analyses unless otherwise specified. The geographic centre of all animals' territories was on the northern side of the fence (left of the middle line in Panel A) and on the eastern side of the river (right of the middle line in Panel B). Numbers of GPS locations were binned within 100-m width bands up to a maximal distance of 5 km from the barrier. See Fig. S1-S4 in the Supporting Information for an enlarged representation of the data distribution of each individual of the four species (Panel C).

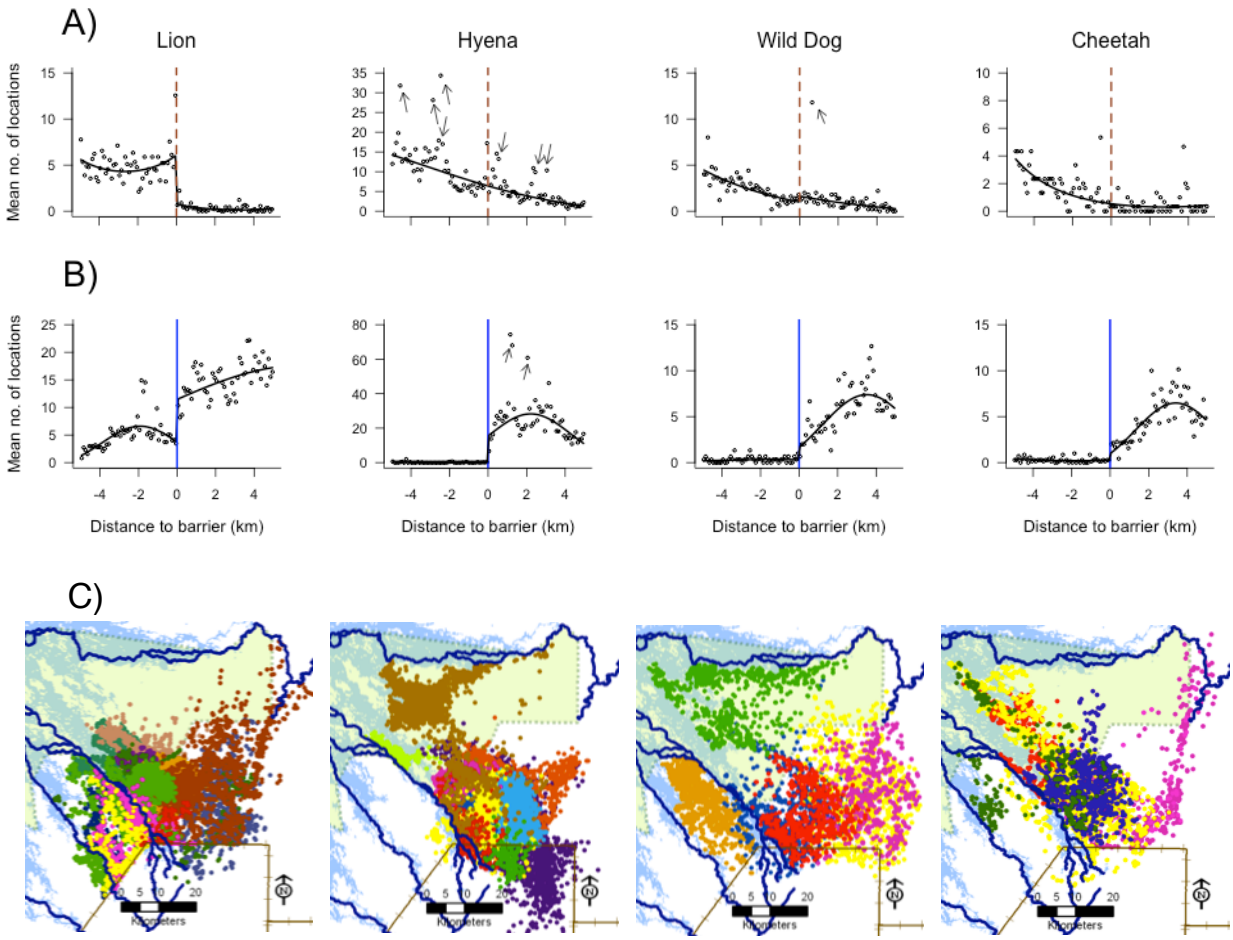
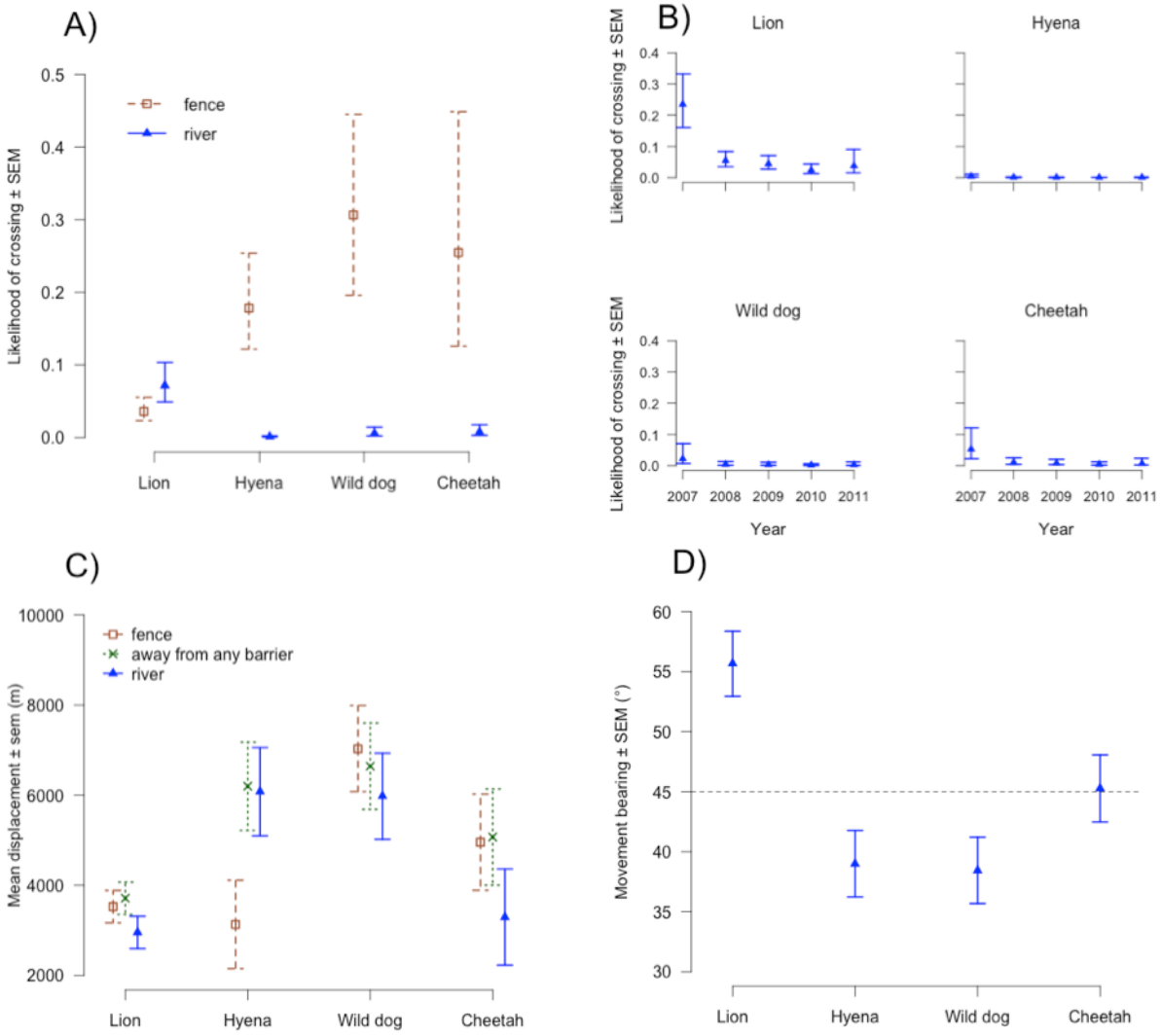


Figure 3: Barrier crossing likelihood and movement metrics for four large carnivore species. Crossing likelihood was investigated by logistic regression for two different barrier types, the fence and the rivers (Panel A), and between years for the rivers (Panel B). Water levels in the rivers constantly increased between 2007 and 2011 due to exceptionally high precipitation. Net displacement between four consecutive 'steps' in the vicinity of the barriers and at random locations away from the barriers (Panel C) and movement bearings in the vicinity of the fence for the four species (Panel D). Values larger than 45° (dashed line) indicate the tendency of movements parallel to the fence, whereas values smaller than 45° indicate the tendency of perpendiculars movements to the fence.



ONLINE SUPPORTING INFORMATION

Hydrology

The Okavango Delta is a highly dynamic hydrological system with water levels changing within and across years as well as between individual rivers. We here highlight some of the main features of the rivers that will help understanding some of the patterns reported in the main text.

The volumes of water in the Gomoti, Santantadibe and Khwai Rivers increased each year during the study period and culminated in a record flood in 2011. Consequently, the proportion of inundated floodplains on both sides of the rivers increased considerably between 2007 and 2011. These changes across years and seasons were, however, not further quantified due to inaccessibility. Nevertheless, the width of the Gomoti River (the river that interested the majority of the study animals) and associated floodplains, was assessed on the base of satellite imagery (Google Earth). Floodplain width was calculated every 500 m moving upstream from the fence and was defined as the distance between the river and the closest riparian tree line (Fig. A). The eastern floodplain had an average width of 457 m (min.: 36; max.: 1766 m) and the western floodplain averaged 1358 m (min.: 54; max.: 2985 m).

The western floodplain of the Gomoti is so substantially larger and more inundated than the eastern floodplain and may thus have been less accessible to animals. This may explain the humped shape of the curve for lions (see Fig 2B in the main text). Lions, which we showed are less affected by the rivers than the other species, may perceives a large and deep floodplain like hyenas, wild dogs and cheetah perceive and are hindered by a narrower and only partially inundated floodplain. Hence the similarity between the humped curve for lions on the western side and the humped curve for the other three species on the eastern side. Lions, however, do not seem to be negatively hindered by the smaller eastern side of the river and this is in line with the overall tendency of lions of being relatively less affected by water bodies. We speculate that the risk associated with predation by crocodiles may be partially

responsible for the differences in crossing likelihood between lions and the other three species. In two occasions we witnessed crocodiles attacking and drowning wild dogs and being considerably larger, lions may be safer from attacks by crocodiles. Such speculation needs however been carefully investigated in the future.

In general, water levels played a significant role in the relative permeability of rivers for all species (see Fig 3B in the main text). For rural communities living in the proximity of rivers characterized by a seasonal changing hydrology, the dry seasons (and more in general years of drought) and the associated low water levels may represent periods of increased conflict with carnivores and wildlife in general.

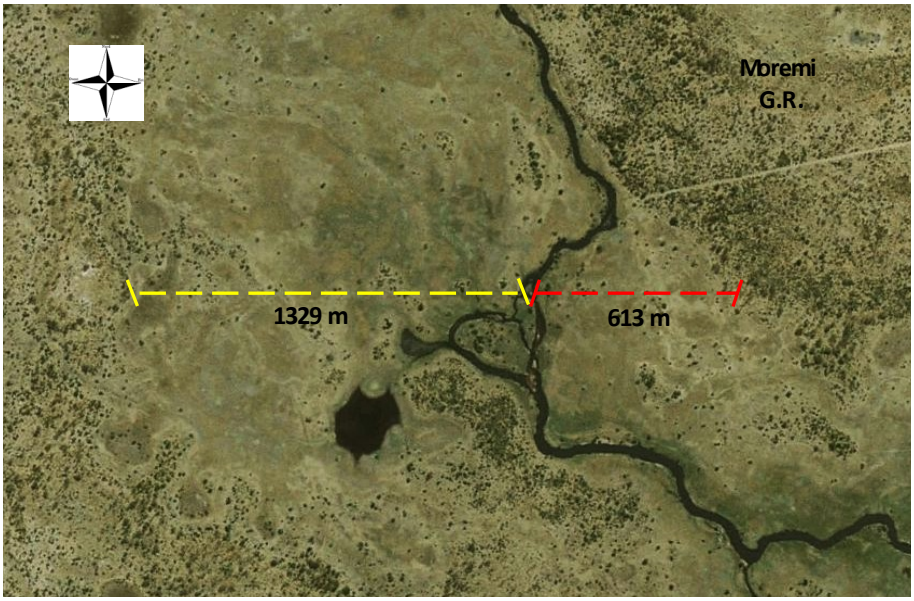


Fig. A: Satellite image of a section of the Gomoti River (visible in dark) and its associated floodplain. The eastern and western width of the floodplain was measured every 500 along the channels and was defined as the distance to the closest, perpendiculat, continuous riparian tree line. For geographical reference, a section of the boundary of Moremi Game Reserve (top right corner) is also visible.

The changing water levels not only influenced river-crossing likelihood but likely also fence-crossing likelihood, especially of lions. During the study period (2007–2011), we drove along the fence on several occasions but did not observe any major damages. The fence was, however, severely damaged where it crossed the three rivers and this was likely due to water-caused rotting of the fence's wooden posts and maintenance impossibility (Fig. B). Almost half of the fence-crossing locations for lions was at the intersections between the rivers and the fence and occurred during periods of low water levels. We believe that, as the water-flow moves southwards across the study area and floodplains slowly dry out, the destroyed sections of the fence are exposed and allow an easy crossing for wildlife, among others lions. An improved maintenance – in the particular case at the intersection between the rivers and the fence – could thus further reduce crossing likelihood consequently reducing conflict with lions.

Fig. B: A damaged section of the fence at the crossing point with the Gomoti River. As the water dries out during periods of low flood levels, damaged section of the fence are exposed and allow an easily crossing for lions.

Tables and Figures

Table S1: Polynomial models for space use across two barrier types as a function of distance to the barrier, distance² (area) and barrier side. Adjusted r^2 (Adj. r^2) for the models are given. Grey fields indicate the combined effects (polynomial effect) of distance and distance² and the respective interaction terms.

FENCE				
Lion				
	Df	F	P	Adj. r^2
Distance	1	844.38	< 0.001	
Distance²	1	1.81	0.182	
Dist_poly	2	419.90	< 0.001	
Side	1	227.35	< 0.001	
Distance:Side	1	13.99	< 0.001	
Residuals	95			0.92
Spotted Hyena				
	Df	F	P	
Distance	1	328.05	< 0.001	
Distance²	1	4.69	0.033	
Dist_poly	2	166.38	< 0.001	
Residuals	97			0.77
Wild Dog				
	Df	F	P	
Distance	1	246.41	< 0.001	
Side	1	7.93	0.006	
Distance:Side	1	2.81	0.097	
Residuals	96			0.72
Cheetah				
	Df	F	P	
Distance	1	88.06	< 0.001	
Distance²	1	18.96	< 0.001	
Dist_poly	2	53.52	< 0.001	
Residuals	97			0.51

RIVER				
Lion				
	Df	F	P	Adj. r^2
Distance	1	563.20	< 0.001	
Distance²	1	14.02	< 0.001	
Dist_poly	2	288.68	< 0.001	
Side	1	27.65	< 0.001	
Distance:Side	1	24.79	< 0.001	
Distance²:Side	1	24.71	< 0.001	
Dist_poly : Side	2	24.76	< 0.001	
Residuals	94			0.87
Spotted Hyena				
	Df	F	P	
Distance	1	2762.64	< 0.001	
Distance²	1	5.65	0.019	
Dist_poly	2	1395.77	< 0.001	
Side	1	1099.86	< 0.001	
Distance:Side	1	8.73	0.004	
Distance²:Side	1	30.97	< 0.001	
Dist_poly : Side	2	20.01	< 0.001	
Residuals	94			0.98
Wild Dog				
	Df	F	P	
Distance	1	877.26	< 0.001	
Distance²	1	12.81	< 0.001	
Dist.tot	2	443.42	< 0.001	
Side	1	105.20	< 0.001	
Distance:Side	1	22.54	< 0.001	
Distance²:Side	1	9.18	0.003	
Dist_poly : Side	2	15.80	< 0.001	
Residuals	94			0.91
Cheetah				
	Df	F	P	
Distance	1	1021.47	< 0.001	
Distance²	1	39.27	< 0.001	
Dist_poly	2	528.63	< 0.001	
Side	1	129.23	< 0.001	
Distance:Side	1	35.89	< 0.001	
Distance²:Side	1	30.02	< 0.001	
Dist_poly : Side	2	32.84	< 0.001	
Residuals	94			0.93

Figure S1: GPS locations of twelve collared lions. Each colour represents an individual; each dot represents a single location. Ticked line = Buffalo fence; dark blue lines = rivers; turquoise areas = floodplains; pale green = Moremi Game Reserve.

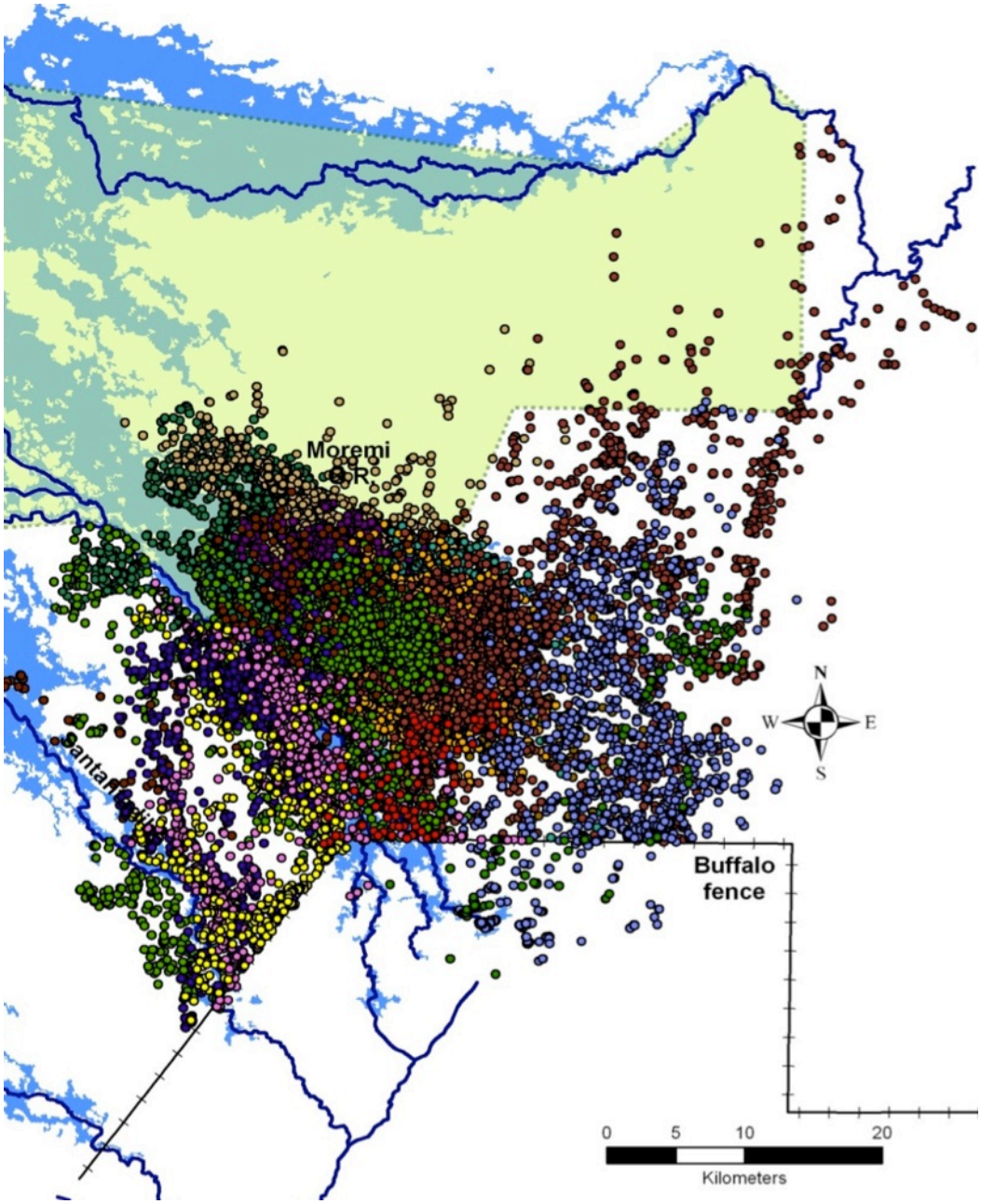


Figure S2: GPS locations of ten collared spotted hyenas. Each colour represents an individual; each dot represents a single location. Ticked line = Buffalo fence; dark blue lines = rivers; turquoise areas = floodplains; pale green = Moremi Game Reserve.

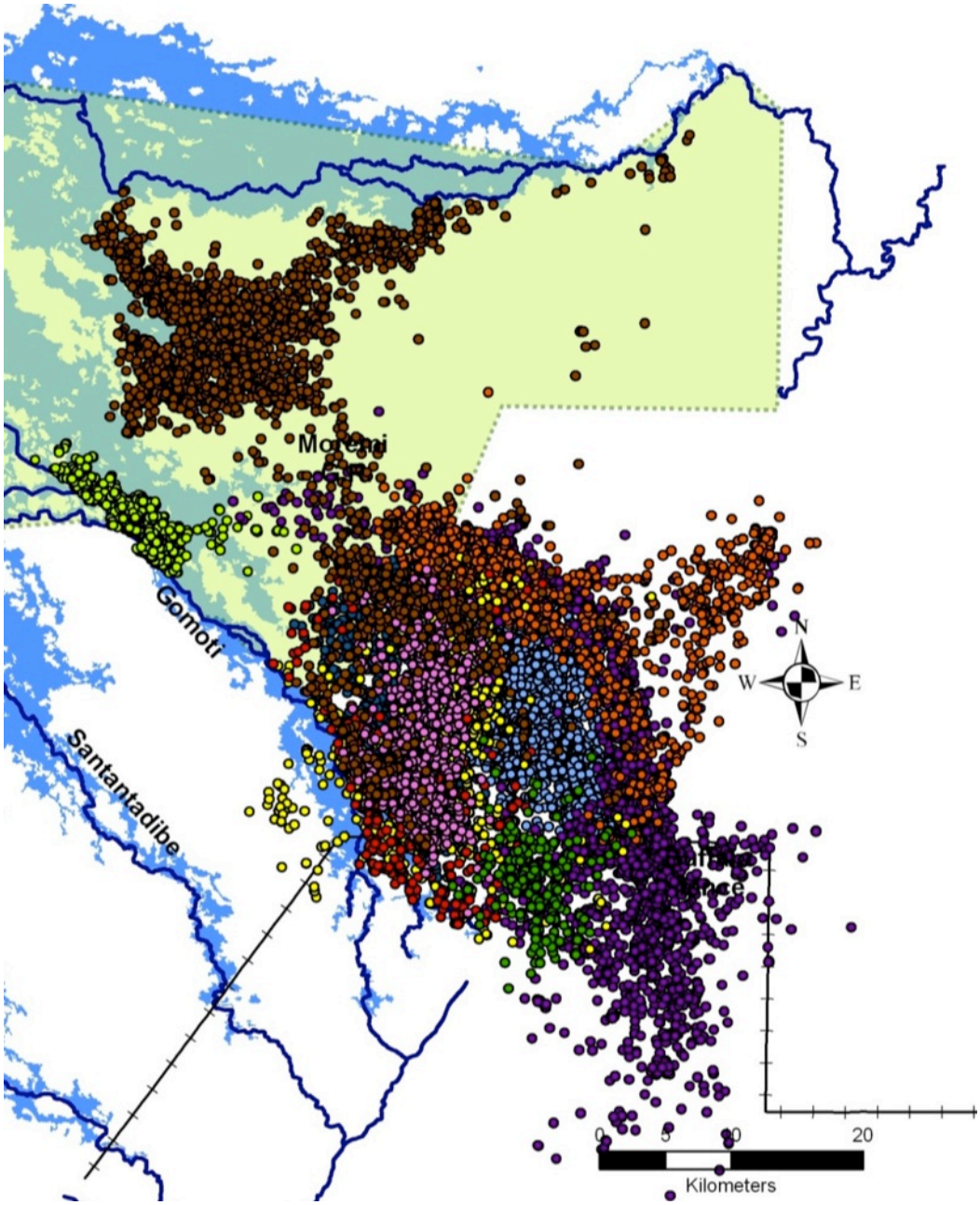


Figure S3: GPS locations of six collared African wild dogs. Each colour represents an individual; each dot represents a single location. Ticked line = Buffalo fence; dark blue lines = rivers; turquoise areas = floodplains; pale green = Moremi Game Reserve.

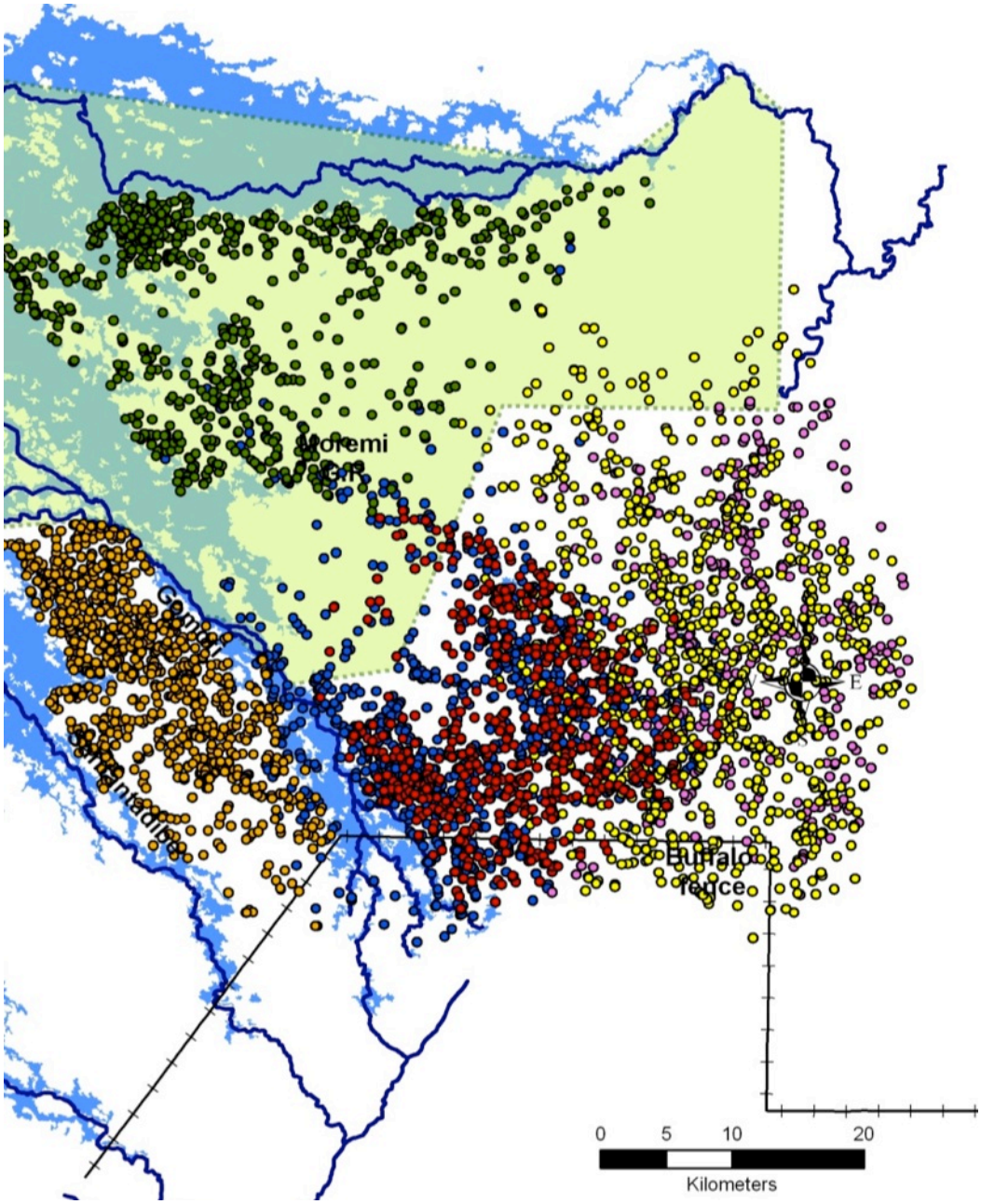
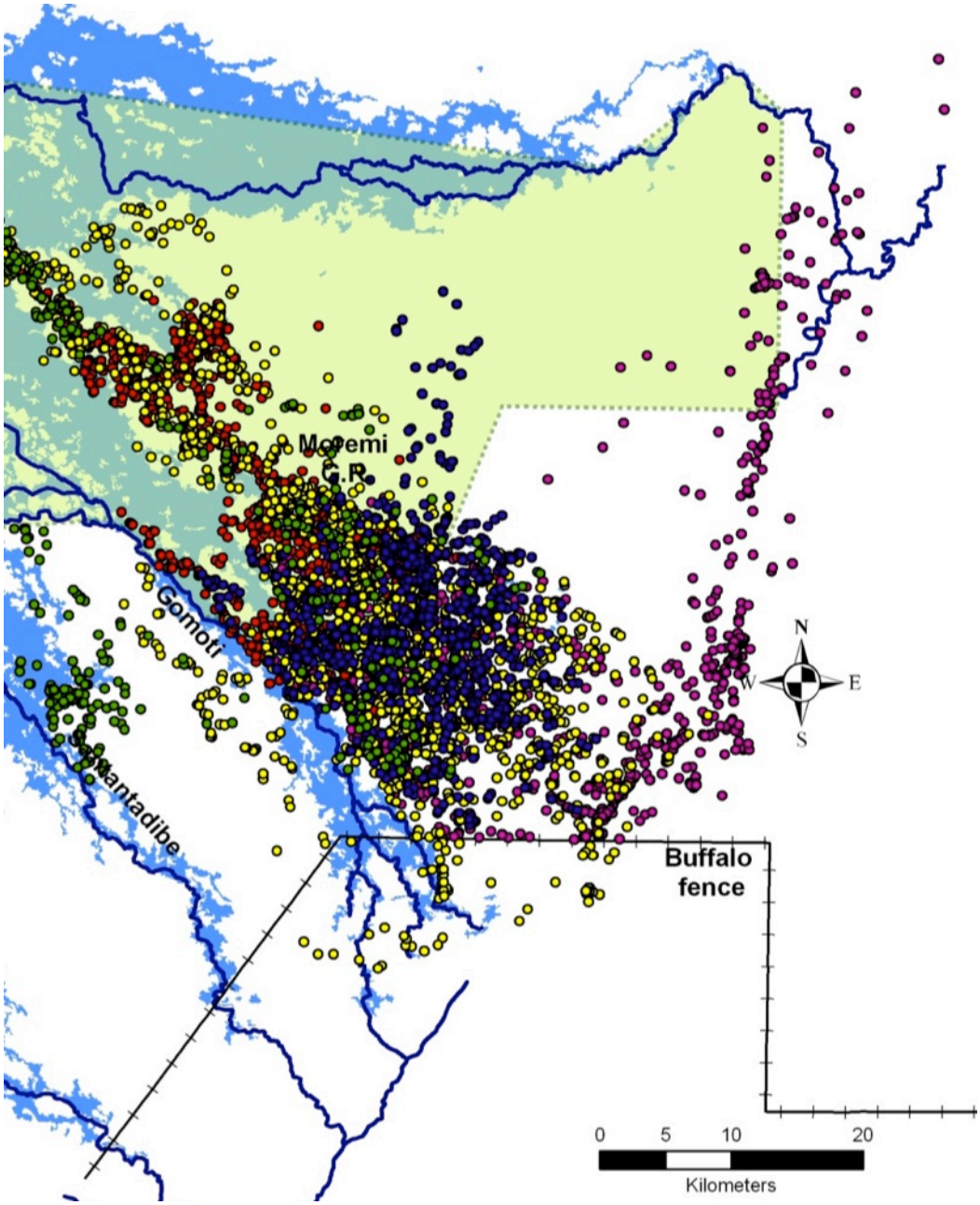


Figure S4: GPS locations of five collared cheetahs. Each colour represents an individual; each dot represents a single location. Ticked line = Buffalo fence; dark blue lines = rivers; turquoise areas = floodplains; pale green = Moremi Game Reserve.



Chapter Five

Density and habitat use of lions and spotted hyenas in northern Botswana and the influence of survey and ecological variables on call-in survey estimation. *Biodiversity and Conservation* (2013)

Top: Preparation of the calling station experiment. Different calls were broadcasted to attract spotted hyenas and lions for survey purposes. The speaker was continuously rotated to ensure 360° sampling.

Bottom: A young male lion investigating a speaker temporarily left on the ground during daytime (Photo courtesy Femke Broekhuis)

Density and habitat use of lions and spotted hyenas in northern Botswana and the influence of survey and ecological variables on call-in survey estimation

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Running Headline: Spotted hyena and lion calling station survey

ABSTRACT

Top predator species significantly impact ecosystem dynamics and act as important indicator species for ecosystem health. Reliable density estimates are therefore necessary for the development of management plans and ecosystem monitoring. This study aims to establish baseline density estimates for two top predators, the spotted hyena and the lion, in the Okavango Delta in northern Botswana. Using the calling station survey technique, we surveyed free-ranging populations of the two species and investigated methodological variables that might influence results on distributions and densities, including habitat variation, seasonality, and different types of playback sounds. Calling stations were distributed over an area covering approximately 1,700 km^2 characterized by three major habitat types: floodplain, mixed acacia sandveld, and mopane woodland. Survey results indicated that spotted hyenas were evenly distributed independent of habitat type and season throughout the entire study area with an overall density estimate of 15.4 adults/100 km^2. In contrast, lion distribution and density varied significantly with differences in habitat and between seasons. Lion density in the prey-poor mopane woodland was negligible, while in the comparatively prey-rich floodplains was estimated at 34.6 individuals/100 km^2. In testing the effect of different playback sounds we found that both species were significantly more likely to respond to calls of conspecifics. Our results show how several factors may influence density estimates and emphasize the importance of standardize methods to allow consistent replication of surveys that can be used for broad-scale monitoring of large predator species.

Key-words: Calling station; *Crocuta crocuta*; density estimate; habitat use; *Panthera leo*; playback sounds.

INTRODUCTION

The effective implementation of conservation strategies and management plans requires systematic assessment of the resources and biodiversity of an ecosystem (Gros et al. 1996, Ogutu and Dublin 1998, Mills et al. 2001, Kiffner et al. 2007, Funston et al. 2010). Reliable density estimates of animal and plant species are necessary, for example, to set sustainable harvesting quotas. Numerous direct and indirect techniques to monitor wildlife populations and evaluate trends and changes have consequently been developed (Neff 1968, Kruuk 1972, Harrington and Mech 1982, Karanth and Nichols 1998, Stander 1998, Gese 2001, Packer et al. 2005, Balme et al. 2009, Chase and Griffin 2009, Funston et al. 2010). However, conventional distance sampling techniques, which are commonly used to survey large mammals, are often inappropriate for top predators that are nocturnal and elusive or occur at low densities (Balme et al. 2009). Adequate techniques to assess the distribution and density of these species need to be developed and implemented.

In carnivore research, camera trapping is rapidly gaining acceptance for estimating distribution and densities of species that are difficult to observe directly but this method requires that individuals can be identified from pictures (Karanth et al. 2006, Stein et al. 2008, Balme et al. 2009, Pettorelli et al. 2010). For species such as lions *Panthera leo* where this is not always the case alternative methods must be used. Spoor surveys have been suggested as one method but their efficacy is substrate- and habitat-specific, making comparisons between sites difficult (Stander 1998, but see Funston 2010). A potentially less biased method are calling station surveys. These have several advantages in comparison to other techniques, including limited equipment, time (multiple calling stations can be conducted per day) and training requirements. Furthermore, calling station surveys can be conducted in various landscapes independent of substrate and habitat specifics and across large areas.

The use of calling stations to estimate the distribution and density of animals is particularly suitable for vocal, territorial animals such as spotted hyenas *Crocuta crocuta* and lions. The method was initially used to survey spotted hyenas in the Serengeti (Kruuk 1972) and then subsequently refined with controls intended to standardize the method for wider use (Mills 1985, Ogutu and Dublin 1998, Mills et al. 2001, Creel and Creel 2002). In calling station surveys density estimates for the focal species are based on the number of individuals responding to broadcast recordings. The method can be used to investigate spatial and temporal variation in density across heterogeneous landscapes and habitats. For example, Mills et *al*. (2001) used calling stations to compare the distribution of hyenas in different vegetation types. The results from the calling station surveys may be compared for validation purposes with cumulative location data of individuals obtained for example from radio collars.

Because different calls convey different messages, the type of call used is likely to influence an animal's response. For example, the calls of a female lion are expected to attract males but also resident territorial females expected to approach to chase the intruder away (McComb et al. 1994, Grinnell and McComb 2001, Ramsauer 2005, Pfefferle et al. 2007). The same calls played to hyenas should leave them indifferent and not attract them, or may even partially hold them back because of the presence of a larger and stronger competitor (Kiffner et al. 2007). Kiffner et *al*. (2007) suggested that species-specific sounds should be played when using calling stations for lions or hyenas, but the degree to which different sounds influence response has not yet been tested. Other aspects, such as individual age and social status, group size and behaviour, may further influence response and need to be considered. For instance, lions on a kill very rarely responded to broadcast calls (Ogutu and Dublin 1998).

We used multiple calling stations over a 3-year period to estimate densities of free-ranging populations of spotted hyenas and lions in Moremi Game Reserve (MGR) and

adjacent Wildlife Management Areas (WMAs) in northern Botswana. For these regions, no previous density estimates were available for spotted hyenas, and the most recent ones for lions were made in 2000 (Winterbach et al. 2002). With the present study, we aim to establish new and more precise estimates for these two top predator species that could be used as baseline for future comparisons and for management purposes. A further goal of our study is to improve the calling station method by comparing its reliability across habitat types, seasons and types of calls. We therefore conducted our calling station survey across three major habitat types. To evaluate seasonal trends in the use of the different habitats, the calling stations were equally divided between the dry and the wet season. We also investigated the response of hyenas and lions to different sounds by broadcasting distinct calls. Finally, we compared our calling-station estimates with data collected from GPS radio-collared individuals.

MATERIAL AND METHODS

Study area

We conducted our study in the Okavango Delta in Northern Botswana, over an area of approximately 1,700 km^2 that comprised the eastern section of MGR and the adjacent WMAs. MGR is not fenced, and animals can move freely between the reserve and the WMAs where the only permitted human activities are photographic and trophy-hunting tourism. The southern boundary of the study area is delimited by an artificial veterinary fence built to control the movements of Cape buffalo *Syncerus caffer* (Fig. 1). The Okavango Delta is a freshwater ecosystem characterized by a mosaic of habitat types such as rivers, swamps, perennial floodplains, seasonal floodplains, grassland, shrub-grassland, grassland dominated by *Acacia*, riparian woodland and woodland dominated by mopane *(Colopospherum mopane)* (Mendelson et al. 2010). The various habitat types support different prey species; in general prey abundance is higher on floodplains and lower in the

mopane woodland, especially during the dry season (Bartlam 2010, G. Cozzi unpubl. data). The region is characterized by a dry season between April and October and a wet season between November and March with average precipitation of 450–600 mm/year (Mendelson et al. 2010).

Habitat data and calling station sites

The different habitats of the Delta were categorized into three major habitat types: 1) floodplains (rivers, swamps, perennial floodplains and seasonal floodplains), 2) mixed acacia sandveld (grassland, shrub-grassland, riparian woodland and acacia-dominated grassland) and 3) mopane woodland. Eighteen calling-station sites were distributed equally within these three habitat types. A site was classified as 'floodplain' if there was a conspicuous percentage (> 10 %) of floodplains within a 3 km radius; a sited was categorised as 'mixed' or 'mopane' if more than 2/3 of the area within a 3 km radius was covered by mixed acacia sandveld or mopane woodland, respectively. The percentage of each vegetation type within a 3 km radius from the calling-station site was calculated in ArcGIS 9.2 (ESRI) using a digital vegetation map provided by the Okavango Research Institute of the University of Botswana. For each site, the distance to the closest camping ground or lodge (the presence of human refuse dumps has been shown to influence the distribution of spotted hyenas; (Kolowski and Holekamp 2008)), the distance to perennial water (natural or artificial) and the distance to the veterinary fence (shown to influence the movement patterns of lions; Cozzi et al. in review) were also calculated (Table 1 and Table S1). The eighteen calling-station sites were roughly positioned on the intersection points of a rectangular 7 x 7 km grid. This distance was used to minimize the chances that an individual could hear playback sounds from more than one calling station at the same time and was based on reports from Mills *et al.* (2001) and Creel & Creel (2002) and on results from calibration experiments conducted during this study (see next paragraph). The exact

location of each site was adjusted to obtain the best possible visibility, which typically was ≥ 50 m.

Calibration experiments

Because not all individuals within the auditory range of a calling station are likely to approach, (Ogutu and Dublin 1998, Mills et al. 2001), 27 calibration experiments were conducted to determine the likelihood and the distance at which animals respond to playback sounds (Table S2). For this, one researcher was stationed with the target individual(s) while a second researcher played the playback sounds at a known distance. Calibration experiments could only be done for lions because in the study area, hyenas were not accustomed to vehicles and it was therefore not possible to observe them during a calibration experiment without influencing their behaviour.

Calibration experiments were carried out in the same way as the subsequent calling-station survey (see below). The responses of the target individual(s) were noted and classified in a dichotomous way as response (vs. no response) if the target individual stopped its activity and paid attention to the calls, and approach (vs. no approach) if the animal was observed at the calling station. Group size, gender, age and behaviour of the target individual(s) were recorded, as well as the time taken to arrive at the calling station. Because of the very low abundance of lions in the mopane woodland (this study) and the consequent difficulty in finding them, very few calibration experiments could be conducted in this habitat (Table S2). For spotted hyenas we used the response distance and likelihood values suggested by other authors (Mills et al. 2001, Creel and Creel 2002). Response likelihood and distance were then used to calculate density for lions and hyenas (see below).

Calibration experiments were used to predict, for any given distance, the time that lions took to approach the speaker and the likelihood that lions hearing the calls would actually

approach. We expected that with increasing distance between the lions and the speaker the variance in the time taken to approach would increase, thus violating the assumption of homoscedasticity. We therefore used a generalized least squares model with 'varExp' variance structure to account for the heteroscedasticity of the data (Zuur et al. 2009). We used a logistic regression to predict the lions' response likelihood as a function of the distance to the speaker.

Calling station survey and call broadcasting

Calling stations were carried out at night, when hyenas and lions are active (Cozzi et al. in press), and started at least half an hour after sunset. Typically, three to four calling-station sites were sampled within one night. The calling stations were carried out under bright moonlight conditions to facilitate the detection of approaching individuals. Spot lights and binoculars were used at regular intervals to scan for eye-shine. All predator species approaching the calling stations were recorded as well as the time since the beginning of the observation period (= experiment). If possible, gender and age of each individual were noted. Experiments were only carried out in the absence of wind; the starting-time and the temperature were also recorded. Experiments were conducted at the end of the rainy season (April–May) and at the end of the dry season (October–November) to investigate seasonal differences.

We used two different sets of calls to test the response of hyenas and lions to different playback sounds. One set of calls, expected to be particularly suitable for attracting hyenas and successfully used in the past (Mills 1998, Mills et al. 2001, Creel and Creel 2002), consisted of several sounds representing the bleating of a wildebeest *(Connochaetes taurinus)* calf, hyenas competing over a kill, a fight between two neighbouring hyena clans and hyenas mobbing lions (the latter were not audible). In this paper we refer to this collection of calls, which collectively lasted six minutes, as 'hyena

calls'. The second set of calls, referred to as 'lion calls', consisted of the roars of a single lioness, the bleating of a wildebeest calf, distress calls of buffalo (*Syncerus caffer*) and hippopotamus *(Hippopotamus amphibious)* and hyenas mobbing lions; these calls collectively lasted ten minutes. The main difference between these two sets of calls was the addition of the roar of a single female lion; we thus expected that the second set of calls would be particularly successful in attracting lions. The combinations of the playback sounds used were chosen to attempt to eliminate potential bias introduced by attracting only hungry individuals, as any resident individual should be attracted to social circumstances such as a territorial dispute or a single intruder (Mills et al. 2001).

Experiments were conducted between 2007 and 2010, and no more than one sampling round of the 18 stations (lasting less than seven nights) using the same set of calls (i.e. hyena calls or lion calls) was carried out per season to minimize habituation of animals to the calls (Table 2). In those years when both hyena calls and lion calls were used during the same season (2008 and 2010, cfr. Table 2), a time span of a month was allowed between the two rounds of the 18 stations. During the broadcasting of the calls the loudspeaker was rotate of 90° at constant time intervals to ensure 360° sampling (Ogutu and Dublin 1998, Mills et al. 2001, Kiffner et al. 2007). The calls were broadcasted at 110 dB at 1 m from the speaker (measured with a PCE-EM882 digital Environmental Meter) through an Apple iPod attached to a 12 Volt Pioneer GM-X332 amplifier connected to an Electrovoice Sx500+ speaker positioned at 1.5 m above ground.

Density estimates

We used data on the number of individuals approaching the calling stations, the maximum distance at which animals responded to the calls (sampling area) and the likelihood of animals approaching (not all individuals hearing the calls will approach) to calculate density estimates for the three habitat types and for the entire study area.

We used the following formula:

$$Density = \frac{number\ of\ individuals\ approaching}{sampling\ area * response\ likelihood} \qquad eq.(1)$$

The time required by hyenas to approach a calling station after a hyena call was 11.2 ± 1.7 min (mean ± S.E.M.), while the time required by lions to approach a calling station after a lion call was 23.7 ± 3.7 min (mean ± S.E.M.). An appropriate broadcasting time was thus necessary to take into account these differences between hyenas and lions, respectively, in their reaction times to playback sounds (Ogutu and Dublin 1998, Kiffner et al. 2007) and give enough time to the individuals within the sampling radius (but not outside it!) to approach the calling station and thus adequately estimate densities. The 6-min-long hyena calls were separated by 4 min intervals of silence and repeated 3 times. To estimate hyena densities, the number of individuals entered in the numerator of equation (1) thus corresponded to the number of hyenas that approached during a full 30-min ((6 + 4) * 3) broadcasting time with hyena calls. The 10-min-long lion calls were separated by 5 min intervals of silence and repeated 4 times. To estimate lion densities, the number of individuals entered in the numerator of equation (1) corresponded to the number of lions that approached during a full 60-min ((10 + 5) * 4) broadcasting time with lion calls.

For lions we used a response likelihood of $\mu_{Li} = 0.4$ at a distance of 2.0 km (this study, see below), resulting in a sampling area of 12.6 km^2 around each calling station. Because we could not calibrate survey distances experimentally for hyenas, we used values from other studies. In the Kruger National Park, Mills *et al.* (2001) considered the response probability up to 3.2 km to be a constant and to be zero beyond that. Surveys in Hluhluwe-iMfolozi Park (Graf et al. 2009) and Selous Game Reserve (Creel and Creel 2002) both considered a response distance of 2.8 km to provide best estimates. We therefore used the weighted mean of the two values ((3.2 km + 2.8 km + 2.8 km)/3 = 2.93 km) as our response distance, giving a sample area of 27.0 km^2 around each calling station. Response

likelihood was estimated in Kruger National Park (Mills et al. 2001) and Hluhluwe-iMfolozi Park (Graf et al. 2009) at 0.61 and 0.60, respectively. For spotted hyenas, we used a response likelihood of $\mu_{SH} = 0.6$ at a distance of 2.9 km.

Preliminary analysis

The spatial auto-correlative structure, among the 18 calling-station sites, of the response variables presence and abundance was tested using Mantel statistics based on Spearman's rank correlation with 1,000 permutations and Euclidian distances as similarity indices (Cozzi et al. 2008) following (Legendre and Legendre 1998). Hyena presence ($r = 0.01$, $p = 0.08$), as well as the number of hyenas approaching the stations ($r = 0.04$, $p = 0.14$) were not spatially auto-correlated, suggesting an even distribution across the study area. Lion presence ($r = 0.07$, $p = 0.03$), and the number of lions responding to the stations ($r = 0.18$, $p = 0.001$) were, however, significantly spatially structured. This spatial structure may have resulted from a corresponding spatial autocorrelation of the habitat types within the study site (see Fig. 1).

Spearman's correlation coefficients between the six geographical predictor variables distance to water, distance to the fence, distance to camps/lodges, percentage of floodplains, percentage of mixed sandveld and percentage of mopane woodland were calculated (Table S3). As proposed by Zuur et al. (2009), the threshold for collinearity among explanatory variables was set at $r = 0.5$. Following this procedure we excluded mixed sandveld, floodplains and distance to fence to avoid collinearity among those variables used in further analysis.

The percentage of each of the three major vegetation types within the core study area of 988 km^2, where a total of 15 lions and 15 spotted hyenas were fitted with GPS radio collars, was compared with the percentage of the recorded GPS fixes within each vegetation type. Floodplains, mixed sandveld and mopane woodland represented,

respectively, 10 %, 58 % and 32 % of this core area. For lions, 8 %, 76 % and 16 % of the GPS fixes collected (N = 43,129) were recorded within floodplains, mixed sandveld and mopane woodland, respectively. For spotted hyenas (N = 33,297 fixes), the corresponding values were 3 %, 75% and 22% (Fig. S1). The majority of the lions within the core area could be individually recognized, and their numbers reached a maximum of 76 individuals in 2010. This value did not consider nomadic individuals and therefore represented a conservative number. The same information was not available for spotted hyenas.

Data analysis

The statistical analyses were performed using the software R 2.13.0 for Windows (R Development Core Group, 2011). Throughout the text, the term 'presence' (respectively 'absence') refers to whether at least one individual approached the calling station; the term 'abundance' refers to the number of individuals that approached. The response variable 'presence' was analyzed for all calling station sites, whereas the response variable 'abundance' was only considered for those sites where at least one individual approached.

We analyzed the response of hyenas and lions to the calling stations, using generalized linear mixed models (GLMM), with a Binomial and Poisson distribution assumed, respectively, for the response variable presence and abundance. Species (hyena and lion), season (dry and wet), type of call (hyena calls and lions calls), percentage of mopane woodland within a 3 km radius around each station, distance to perennial water, distance to lodges/camps and year were treated as fixed explanatory terms; calling station identity was treated as random term. Unless otherwise specified (e.g. for the estimation of the density), for the analysis of presence and abundance, we only considered individuals that approached during the first 30 min of a 60-min broadcasting time with lion calls. This was done to allow direct comparison with the approaches of the two species during the 30-min broadcasting times with hyena calls. Model simplification starting from a full model

followed a backward-selection procedure based on the Akaike Information Criterion (Zuur et al. 2009). Start time and temperature at the beginning of each broadcasting time were also recorded and entered as single explanatory terms in analyses with presence and abundance of hyenas or lions as response variables. Neither start time nor temperature showed any relationship with the response variables, indicating that they did not introduce any biases in the data. Start time and temperature were consequently not included in the above GLMM models to reduce model complexity.

RESULTS

A total of 244 spotted hyenas and 67 lions were observed approaching the calling stations (Table 3). Hyenas were recorded at 71 (54.8 %) of the total 132 calling station experiments, while lions were recorded only on 22 (16.7 %) occasions (Table 3). The number of hyenas and lions approaching the calling stations ranged between 0–15 and 0–13 individuals, respectively, and varied between the three major habitat types (Table 3 and Fig. S2). Particularly striking was the absence of lions at stations in the mopane woodland and this contrasted sharply with lions approaching calling stations in floodplain habitats.

Only four lions that approached the stations were individuals that had not previously been identified during the course of this study. Of the 61 lions whose gender could reliably be determined 32 were males and 29 females. Males were present at 20 (90.9 %) of the 22 occasions where lions were recorded, while females approached on only 12 (54.54 %) occasions, and only on two of these occasions were the females that approached not accompanied by at least one male. In 5 cases male and in 2 cases female lions approached during one of the 30-min-long broadcasting times with hyena calls (N = 62). These figures suggest that male lions are generally more likely to respond to calling stations than females. Similar information could not be collected for hyenas due to the difficulty of identifying and sexing individuals in the field.

Calibration experiments — lion response time, distance and likelihood

We conducted 27 calibration experiments to measure the response time and the response likelihood of lions (Table S2). The average time needed to approach the calling stations significantly increased with increasing distance from the loudspeaker and was significantly different between floodplains and mixed acacia sandveld (distance by vegetation interaction term, $F_{1,10} = 13.49$, $p = 0.006$; Fig. 2A). Whether time to approach varied between the mopane woodland and the other two vegetation types could not be determined because lions could only be rarely (n = 3) located in this habitat type. Averaged over all (including mopane) vegetation types (n = 27), time to approach was 56.3 min (C.I. 48.5–64.0) at a distance of 2 km (Fig. 2A). When the distance from the speaker exceeded 1.5 km, the time to approach varied considerably, while it was almost perfectly linear below this threshold (Fig. 2A). This suggests that over longer distances the motivation to approach varied considerably, which also had direct consequences regarding the time taken to approach.

The likelihood of lions to respond to calls was investigated by logistic regression and analysed as a function of the distance to the speaker. Lions consistently approached if they were at a distance of less than 1.5 km from the speaker, while their response was more unpredictable above this distance (Fig. 2B and Table S2). Their likelihood to respond decreased significantly ($\chi^2 = 3.89$, $p = 0.02$) with increasing distance; it was 46 % (C.I.: 26–67 %) at 2.0 km, where the C.I. intervals were at the narrowest (Fig. 2B). We did not detect significantly different response likelihoods between the different vegetation types (either with mopane included or excluded in the analysis). In those cases where lions approached the speaker, on average 86.1 ± 7.3 % (mean ± S.E.M.) of the focal individual(s) did approach (some individuals remained behind, particularly when retaining a kill; see Table S2). Assuming this value to be a constant over the entire response range,

our results yielded an overall response likelihood for individual lions of $\mu_{Li} = 0.46 * 0.86 = 0.40$ at 2.0 km.

Presence and abundance

Significantly more hyenas responded to the calling stations than lions ($F_{1,228.2} = 58.55$, $p < 0.001$; Fig. 3) and calling stations were more often approached in the dry than in the wet season ($F_{1,14.9} = 9.18$ $p < 0.009$). The differences between seasons depended on the amount of mopane woodland surrounding a calling-station site (interaction season by mopane $F_{1,16.7} = 8.80$, $p = 0.009$): both species showed a negative relationship with the percentage of mopane woodland during the dry season, while during the wet season this relationship was positive (Fig. 3). Based on the assumption that the presence of animals at calling stations is a function of their geographical distribution, this suggests that large areas of mopane woodland may represent a suboptimal habitat type and particularly during the dry season, while animals seem to venture slightly more often into the mopane during the wet season (Fig. 3). The presence of hyenas and lions at the calling-station sites furthermore significantly decreased with increasing distance to the closest lodge/camp ($F_{1,15.8} = 7.90$, $p = 0.013$). Our model did not detect significant differences between years, enabling us to rule out habituation events as a possible source of bias in the presented results.

The numbers of hyenas vs. lions (i.e. response variable abundance) arriving to the calling-station sites depended on the type of call used to attract animals, i.e. hyenas responded better to hyena calls and lions better to lion calls (interaction species by call $F_{1,71} = 8.06$, $p = 0.006$; Fig. 4). This result demonstrates that when investigating animal abundance, the type of call used can be relevant and should be taken into consideration to avoid misleading results. We observed a significant difference in the number of hyenas vs. lions arriving to the calling-station sites in relationship to the distance to the closes

lodge/camp (interaction species by distance to lodge/camp $F_{1,81} = 4.27$, $p = 0.042$); this was due to a strong positive effect for hyenas.

Estimating densities for the study area

Using information on the number of individuals approaching the calling stations, the maximum distance at which animals approach and the likelihood of approach, we were able to calculate densities for the study area and for the different habitat types (Table 4). Mean spotted hyena density was estimated at 15.4 adults/100 km^2 and showed little difference between the three habitat types with 16.9, 16.7 and 12.3 adults/100 km^2 for floodplains, mixed sandveld and mopane woodland, respectively. In contrast, the density of lions differed considerably between habitat types, ranging from an almost complete absence in mopane woodland to an estimated density of 34.6 individuals/100 km^2 in floodplains (Table 4). Density estimates changed considerably depending on the type of call used to attract animals (Table 4).

DISCUSSION

We used a relatively quick and inexpensive method — the calling station method — to survey spotted hyenas and lions in Northern Botswana. The results allowed us to derive habitat-specific density estimates for hyenas and lions in a 1,700 km^2 area in the Okavango Delta. We could also identify seasonal differences in habitat preferences and the effects of different types of calls on the response of the animals. Environmental and geographical factors influenced the presence of animals at calling stations, whereas the type of call used was the main factor influencing the total number of individuals recorded at the calling stations.

Our density estimates for lions are considerably higher than the values reported by Winterbach et al. (2002) for the Okavango Delta (minimum 1.0 and maximum 11.2

adults/100 km^2 before correction for response likelihood). These different results may be attributed to three potential causes. First, Winterbach et al. (2002) considered a sampling radius of 3–4 km and a response likelihood of 60 %, which according to our tests could have overestimated the area sampled. Our values for response distance and likelihood were more similar to values suggested by Ogutu and Dublin (1998) (response likelihood of 25 % at 2.5 km), corresponding to an area with a radius of 2–2.5 km around calling stations. Second, the types of calls broadcast by Winterbach et al. (2002) differed from the ones we used in that they did not include lion vocalizations in their playback sounds. Third, because of logistical constraints (limited roads and the inaccessibility of areas due to flooding) we could only survey about 13.5 % of the study area, less than the recommended 20 % of the total area suggested by (Ogutu and Dublin 1998). The relatively limited sample size may have introduced uncertainty into our results. Reliable density estimates for lions are therefore likely to lie somewhere between our estimates and the values proposed by Winterbach et *al.* (2002). The discrepancies between the two studies indicate the degree of accuracy of the calling station method, which, despite providing a quick, efficient way to estimate densities, needs to be complemented by alternative methods if more precise density estimates are required. In our case, using density estimates of 34.6, 14.1 and 0 lions/100 km^2 for, respectively floodplain, mixed sandveld and mopane, an estimated total of 114 individuals is calculated for the 988 km^2 core area within which the known study population reached a total, conservative count of 76 individuals (see above). No hyena densities have previously been estimated for the Okavango Delta and no comparison was therefore possible. However, our estimates of 16.9, 16.7 and 12.3 hyenas/100 km^2 for, respectively, floodplains, mixed sandveld and mopane woodland obtained with the calling station method are consistent with densities from other study sites showing a comparable prey base and vegetation structure, such as the Kruger National Park in South Africa (Mills, Juritz et al., 2001; mopane woodland: 11.9 hyenas/100 km^2, mixed sandveld: 21.1

hyenas/(100 km^2) and in the Selous national park in Tanzania (Creel and Creel, 2002; 30 adult hyenas/100 km^2).

Our results further showed that lion distribution and density varied considerably among different habitat types, while spotted hyenas were more homogeneously distributed throughout the study area. In prey-rich floodplains, lion density was comparable with the density of the prey-rich areas of eastern Africa (Ogutu and Dublin 1998), while it dropped to near zero in the mopane woodland. The negligible density of lions in mopane woodland is consistent with the low density of prey species and is in sharp contrast to the prey-rich areas associated with floodplains, where we recorded the highest number of lions approaching the calling stations (see Table 3, Fig. S2). This result is consistent with previous studies, which showed a direct relationship between the abundance of lions and the abundance of their prey species (Ogutu and Dublin 1998, Carbone and Gittleman 2002, Ogutu and Dublin 2002, Hopcraft et al. 2005). Spotted hyenas were also recorded at lower densities in the mopane woodland during the dry season, coincident with the lowest number of prey species (G. Cozzi, unpubl. data), thus supporting the positive association between hyenas and prey species (Cooper et al. 1999, Trinkel et al. 2004, Höner et al. 2005).

Our findings emphasize the importance of mopane woodland for the distribution of the two species, in particular lions. We showed that lions are almost absent from large patches of mopane woodland and we conclude that they may only use edges, and particularly during the wet season when relatively more ungulates are present (Bartlam 2010). These results are consistent with location data from lions fitted with GPS radio collars, which show that, although lions sometimes venture into mopane woodlands, they use this habitat type less frequently than the other two vegetation types (Cozzi et al. in prep., and Fig. S1-S3). Considering that mopane woodland is characterised by a sharp boundary with adjacent habitat types (with negligible succession), large patches of mopane

woodland may even represent a type of barrier to territory expansion of lions. Mopane woodland characterises vast areas of northern Botswana and the low lion density in this habitat must be taken into account when extrapolating population estimates to broad landscapes using densities derived from different habitats. Other predator species whose density is not directly linked to prey density (Mills and Gorman 1997) and which suffer from direct predation and competition by lions, such as the African wild dog *Lycaon pictus* (Creel and Creel 1996), may consequently find a spatial refuge (Durant 1998) in the prey-poor mopane woodland.

Our results suggest that different types of calls attract animals differently and highlight the need to have a standardized set of calls, depending on the target species being surveyed (Kiffner et al. 2007). During the calibration experiments, we observed that lions responded noticeably to the 'lioness roar' (lions repeatedly lifted their head every time the lioness was broadcasted, while they very often ignored all other playback sounds) and we therefore consider this playback sound critical. While we assumed that sounds would spread equally between different habitat types and that the response would therefore be constant (an assumption corroborated by the fact that in our calibration experiments we did not detect significant differences in the response likelihood between the three different habitats), further observations are needed to investigate sound attenuation within different vegetation types. Nevertheless, the relatively limited response radius that we used for our calculations (2 km) leads us to believe that we were sampling well within the maximum audible distance for each vegetation type. While reviewing the literature, we observed an inconsistency in broadcasting volume among the various studies. Some studies did not report the broadcasting volume (Mills et al. 2001, Winterbach et al. 2002), some played calls at 'maximum volume' (Ogutu and Dublin 1998, Kiffner et al. 2007) and some at 103 dB (Creel and Creel 2002). Given that the dB scale is a logarithmic scale, a difference of a

few dB will make a big difference; for example, a 10 dB change is a ten-fold change in the power ratio, and 3dB corresponds to about a two-fold change in power ratio.

There is an urgent need of standardize the calling station method to allow for comparisons over different years and among different study areas, and to avoid misleading results. On the basis of previous studies (Ogutu and Dublin 1998, Mills et al. 2001, Creel and Creel 2002, Winterbach et al. 2002, Kiffner et al. 2007) and our own results we can make six recommendations: 1) a standardized set of calls, specific for each target species, should be developed by scientists active in this field of research; 2) response distance and likelihood should be investigated separately for different habitat types; 3) broadcasting volume should be standardised at 110 dB, as this is well within the natural pressure levels of the two species (Durant 2000, Webster et al. 2012) and is easily achieved by the modern equipment (speakers and amplifiers); 4) the length of broadcasting time may be of 30 minutes when surveying hyenas but should be extended to 60 minutes when surveying lions; 5) the response distance for hyenas can be up to 3 km but for lions should be less than 2.5 km; 6) the sampling area calculated with these radii should include at least 20 % of the study area.

Due to increasing human population sizes and human pressures on resources, wildlife is increasingly forced into smaller areas with more severe boundaries, resulting in an increasing need to actively manage valuable wildlife resources. Reliable population estimates for top predators in different regions and habitat types is paramount to the development of management action plans. Results from this study emphasise the importance of standardizing survey methods to avoid intrinsic sources of uncontrolled variance in the calling station method, a method that is increasingly used for monitoring purposes and which is providing results upon which conservation and management decisions and practices are being based.

ACKNOWLEDGEMENTS

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TABLES AND FIGURES

Table 1: Characteristics of the 18 calling-station sites. Distances are given in km. Floodplains, mixed sandveld and mopane woodland coverage within an area of 28.3 km^2 (3 km radius) around each calling-station site is given in km^2; values in brackets represent percentages.

	Mean	SD	Min	Max
Distance to closest calling station	8.4	1.3	7.3	12.22
Distance to water	6.5	7.0	0.1	20.5
Distance to fence	22.9	13.5	0.1	45.4
Distance to camps	6.4	4.1	6.3	13.4
Floodplain	4.8 (16.9)	7.2	0.0	18.7
Mixed	13.7 (48.3)	8.3	1.8	28.2
Mopane	9.8 (34.8)	9.6	0.0	26.5

Table 2: Temporal distribution of the calling station effort. Calling stations were sampled using 'hyena calls' (H) and 'lion calls' (L) (see text for details of the two types of calls). Numbers in brackets represent the number of calling stations used in each trial (in some cases some stations could not be visited due to inaccessibility). Each year, no more than two round of the 18 stations with the same type of calls were performed to minimize habituation events. [1)] April; [2)] May; [3)] October; [4)] November; [*)] data presented in Webster (2008).

Year	2007		2008		2009		2010	
Season	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Calling station		H (13)*	H (14)[1] L (16)[2]	H (18)[3] L (18)[4]		L (18)	H (17)[2] L (18)[1]	

Table 3: Spotted hyenas and lions recorded at calling station sites. The calling stations were located in three main habitat types: floodplains, mixed sandveld and mopane woodland. The column 'Presence' reports the number of times individuals approached the calling stations; the numbers in brackets are percentages (= 'Presence' / N * 100). The column 'Abundance' reports the total number of individuals that approached the calling stations; the number in brackets represents the average number of individuals per calling station if only those calling station occasions where animals were observed were considered (= 'Abundance' / 'Presence').

	Spotted hyena		Lion	
	Presence (%)	Abundance (/station)	Presence (%)	Abundance (/station)
Floodplain (N=42)	28 (66.7)	85 (3.0)	14 (33.3)	49 (3.5)
Mixed sandveld (N=48)	29 (60.4)	97 (3.3)	7 (14.6)	17 (2.4)
Mopane (N=42)	14 (22.6)	62 (4.4)	1 (2.4)	1 (1.0)
TOTAL (N=132)	71 (53.8)	244 (3.4)	22 (16.7)	67 (3.1)

Table 4: Spotted hyena and lion density estimates as a function of type of call and habitat type. All calling-station occasions (N = 132) have been considered as independent data points (averaging numbers per station did not change the estimates and the data are not presented here). The parameters used to calculate densities are as follow: [1)] Response time 30 min; response distance 2.93 km; response likelihood 0.6 (parameters from the literature). [2)] Response time 60 min; response distance 2 km; response likelihood 0.4 (parameters from this study). [3)] Response time 30 min; response distance 1.25 km; response likelihood 0.75 (parameters from this study).

Species	Type of call	Habitat	Density estimate (/100km2)
Spotted hyena	Hyena calling station (N = 62) [1]	Overall	15.4
		Floodplain	16.9
		Mixed	16.7
		Mopane	12.3
	Lion calling station (N = 70) [1]	Overall	7.8
		Floodplain	13.9
		Mixed	8.2
		Mopane	6.4
	All calling stations combined (N = 132) [1]	Overall	11.4
		Floodplain	12.5
		Mixed	12.5
		Mopane	9.1
Lion	Lion calling station (N = 70) [2]	Overall	16.2
		Floodplain	34.6
		Mixed	14.1
		Mopane	0.0
	Hyena calling station (N = 62) [3]	Overall	4.4
		Floodplain	12.9
		Mixed	0.0
		Mopane	1.4
	All calling stations combined (N = 132) [3]	Overall	11.5
		Floodplain	25.9
		Mixed	8.5
		Mopane	0.6

Figure 1: The study area was situated in the Okavango Delta in northern Botswana and comprised a section of Moremi Game Reserve and the adjacent Wildlife Management Areas (WMA). The southern boundary of the study area was defined by the Southern Buffalo Fence (ticked line). Eighteen calling-station sites were sub-divided across three major habitat types on a 7 by 7 km grid and moved to the closest suitable road: six stations (blue stars) were located in the vicinity of floodplains (pale blue), six stations (green circles) in mixed sandveld (green) and six stations (brown quadrats) in the mopane woodland (brown). Blue lines represent rivers, brown lines roads and the dashed line the boundary of Moremi GR.

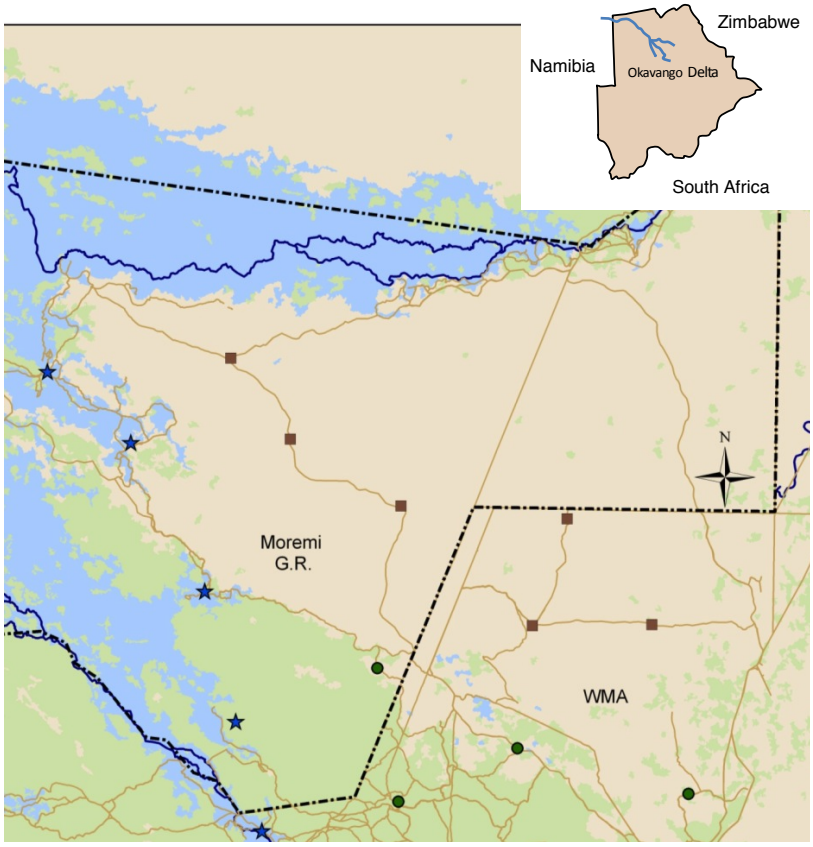


Figure 2: Linear relationship (A) between the time taken to approach the speaker and the distance to the speaker for lions and logistic relationship (B) between the likelihood to approach the speaker and the distance to the speaker for lions. Solid line = overall fitted values; grey area = 95 % CI; dotted line = fitted value for floodplains; dashed lines = fitted values for mixed sandveld; no fitted lines are presented for mopane due to the limited sample size. Jittering has been introduced in (B) for the representation of the raw data (open symbols) to avoid overlapping data points.

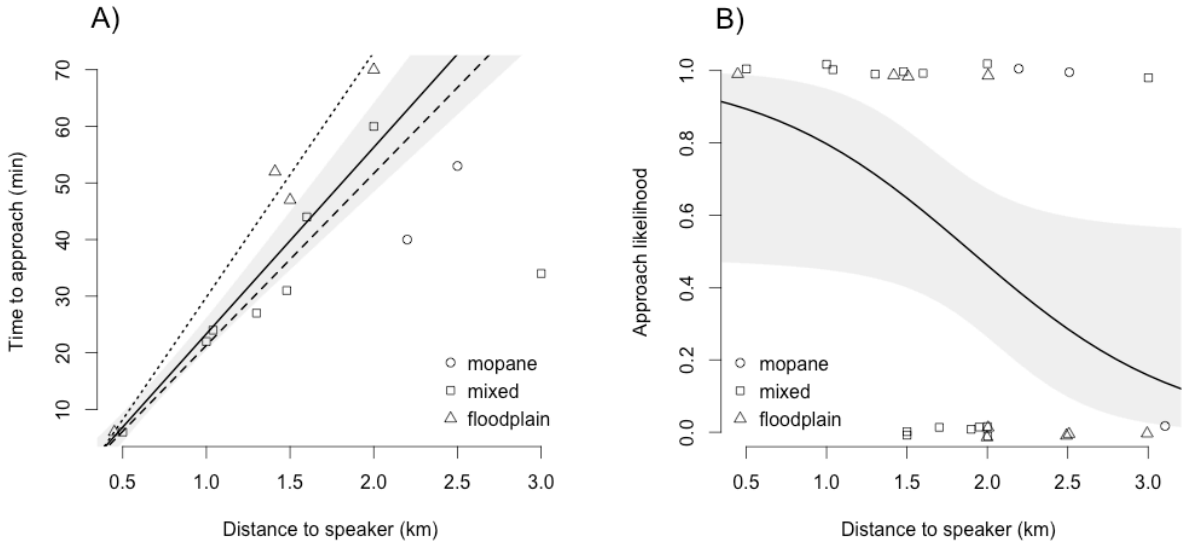


Figure 3: Fitted values (solid line) and 95 % confidence intervals (dashed lines) for the logistic relationship between the presence of (A) spotted hyenas or (B) lions and the percentage of mopane woodland surrounding a calling-station site within a radius of 3 km. Solid line = wet season; dashed line = dry season; grey area = 95 % CI. For this graphical representation distance to camp has been set to be equal to the median distance between the stations and the closest camp.

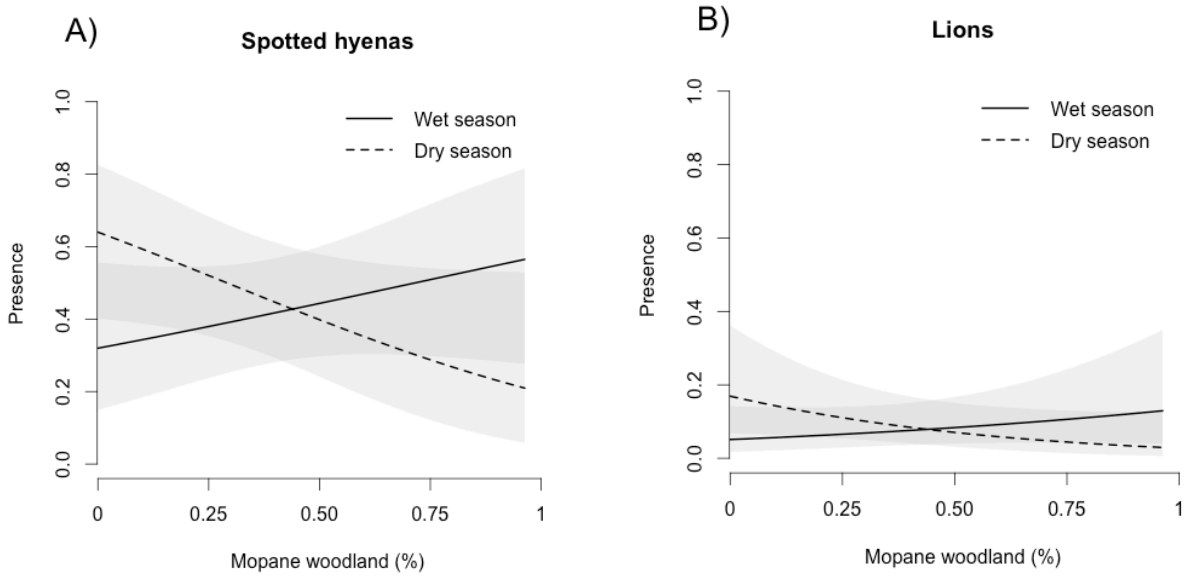
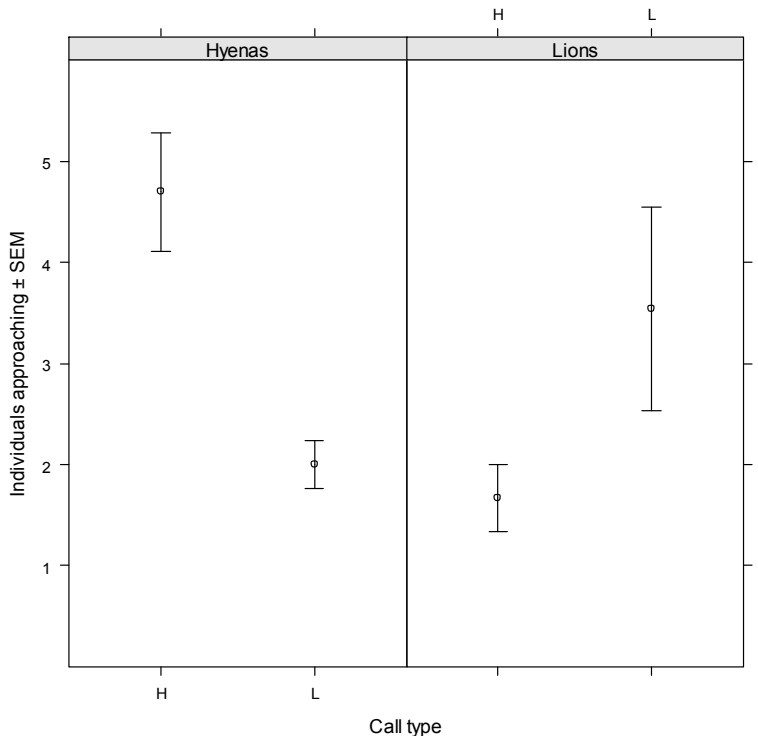


Fig. 4: Mean number of spotted hyenas and lions approaching the calling stations as a function of the type of call used. H = hyena calls characterized by distress calls of prey species and hyena calls. L = lion calls characterized by distress calls of prey species and calls of a single female lion.



ONLINE SUPPORTING INFORMATION

Tables and Figures

Table S1: Characteristics of the 18 calling-station sites. For each site, the amount of floodplains, mixed sandveld and mopane woodland totalled 28.27 km^2, which represented the area sampled around each site (3 km radius). The distances of each site to the nearest lodge/camp (tocamp), to the nearest perennial water source (towater) and to the fence (tofence) are also given.

Location ID	Habitat	Mopane (km^2)	Floodplain (km^2)	Mixed (km^2)	Tocamp (m)	Towater (m)	Tofence (m)
DryPan	Floodplain	0.00	13.38	14.90	8575	200	18311
LionResearch	Floodplain	0.02	9.69	18.56	3257	100	10532
BackyardPan	Mixed	0.06	0.00	28.21	627	8188	12419
GomotiFence	Floodplain	0.08	12.53	15.66	8258	50	178
HuntersRoad	Mixed	4.34	0.00	23.93	5016	4349	4543
FlyCamp	Mixed	2.14	0.00	26.13	7717	12358	7562
SavannaRoad	Mixed	6.95	0.00	21.33	9338	17052	16257
SouthGate	Mixed	6.11	0.00	22.17	2623	10108	21641
MopaneW	Mopane	18.20	0.00	10.08	8522	20453	24762
MopaneE	Mopane	21.27	0.00	7.00	7646	13	24923
MankweCutline	Mopane	19.19	0.00	9.08	13362	17258	32188
HuntingCamp	Mixed	11.54	0.00	16.73	3111	1720	13245
XiniLagoon	Floodplain	4.01	18.66	5.61	1696	50	27582
KuduPlains	Mopane	26.45	0.00	1.82	10319	11895	32884
Budumatau	Floodplain	4.03	13.84	10.41	1519	50	38848
Halfwaypan	Mopane	25.06	0.00	3.21	11790	8660	37374
Fourthbridge	Floodplain	4.41	17.67	6.20	703	50	45425
Xakanakafork	Mopane	23.32	0.00	4.96	10574	3696	43210

Table S2: Number of lions approaching the speaker during calibration experiments to identify the response distance and response likelihood. The distance between the focal individual(s) and the speaker, the number of the focal individual(s), their activity at the beginning of the experiment, the time needed to approach the speaker, the number of individuals approaching the speaker (values in brackets are percentages) and the type of vegetation where each experiment took place are given.

Distance (km)	Nr. individuals	Activity	Vegetation	Nr. approaching (%)	Approaching time (min)
0.45	13	resting	floodplain	13 (1.00)	6
0.50	11	unkn	mixed	10 (0.91)	6
1.00	unkn	unkn	mixed	3 (NA)	22
1.04	4	resting	mixed	4 (1.00)	24
1.30	unkn	unkn	mixed	1 (NA)	27
1.41	8	feeding	floodplain	1 (0.13)	52
1.48	1	resting	mixed	1 (1.00)	31
1.50	3	resting	floodplain	3 (1.00)	47
1.50	1	resting	mixed	0 (0.00)	-
1.50	8	walking	mixed	0 (0.00)	-
1.60	5	walking	mixed	4 (0.80)	44
1.70	1	resting	mixed	0 (0.00)	-
1.90	5	resting	mixed	0 (0.00)	-
1.95	7	resting	mixed	0 (0.00)	-
2.00	12	resting	floodplain	0 (0.00)	-
2.00	1	resting	mixed	0 (0.00)	-
2.00	2	resting	mixed	2 (1.00)	60
2.00	1	resting	floodplain	0 (0.00)	-
2.00	6	resting	floodplain	6 (1.00)	70
2.00	2	resting	mixed	0 (0.00)	-
2.20	2	feeding	mopane	1 (0.50)	40
2.50	2	walking	mopane	6 (1.00)	53
2.50	5	feeding	floodplain	0 (0.00)	-
2.50	9	resting	floodplain	0 (0.00)	-
3.00	2	resting	mixed	2 (1.00)	34
3.00	4	resting	floodplain	0 (0.00)	-
3.10	2	hunting	mopane	0 (0.00)	-

Table S3: Spearman's correlation coefficients between predictor variables of the 18 calling station sites

	Distance to water	Distance to fence	Mopane	Mixed	Floodplain
Distance to camps	0.5	0.1	0.6	-0.3	-0.5
Distance to water		0	0.4	0.1	-0.6
Distance to fence			0.6	-0.8	0.1
Mopane				-0.7	-0.5
Mixed					-0.2

Figure S1: Barplot showing the percentage of each vegetation type within the core area of 988 km^2 and the percentage of the GPS data recorded by radio collars fitted on 15 lions and 15 spotted hyenas that fell within each vegetation type. Fewer GPS fixes than would be expected under the assumption of a random distribution were recorded in mopane woodland and floodplains. The numbers above the bars represent actual percentage values. Shadings represent the percentage of the GPS locations within each habitat type during the dry and wet season.

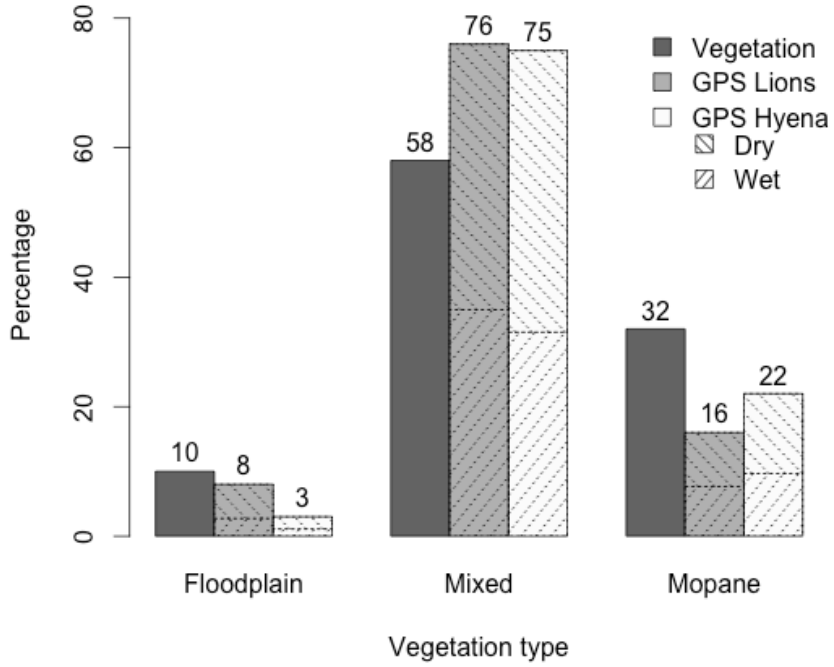


Figure S2: Map showing the mean number of lions (black bars) and hyenas (grey bars) recorded at each calling station site. Calling stations are distributed across three main habitat types: floodplains (pale blue), mixed sandveld (green) and mopane woodland (brown). Blue lines represent rivers, the dashed line represents the boundary of the Moremi Game Reserve and the ticked line shows a veterinary cordon fence.

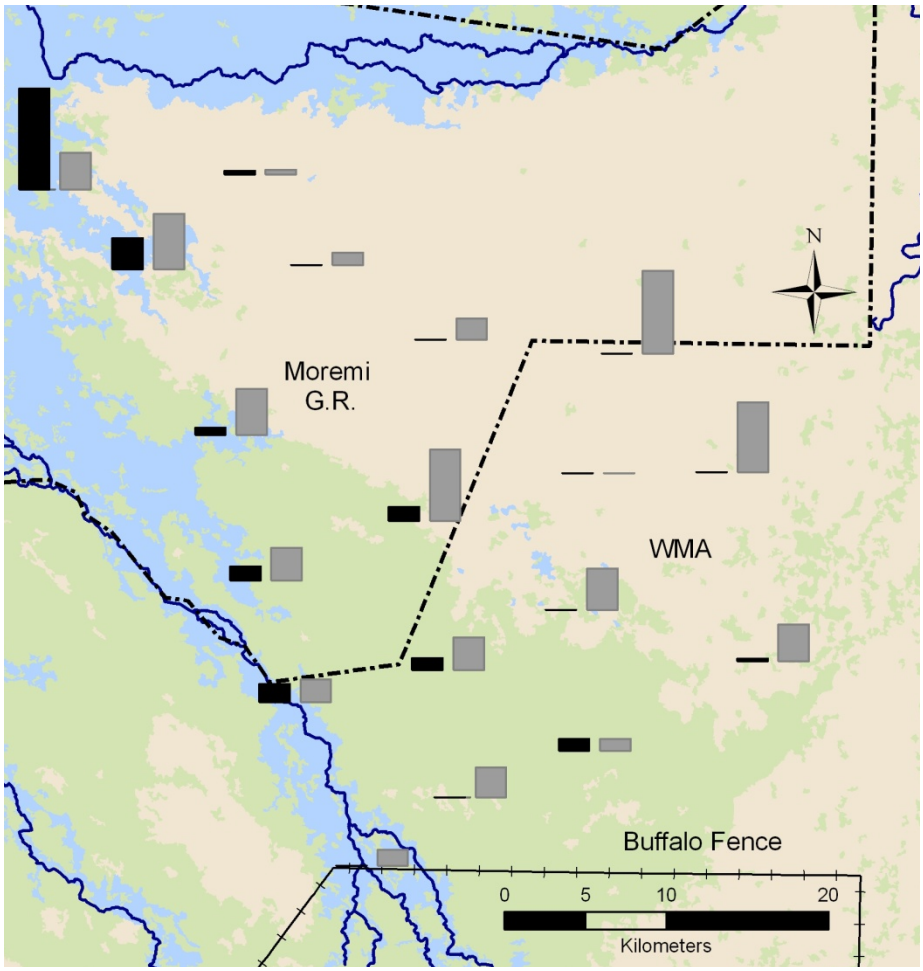
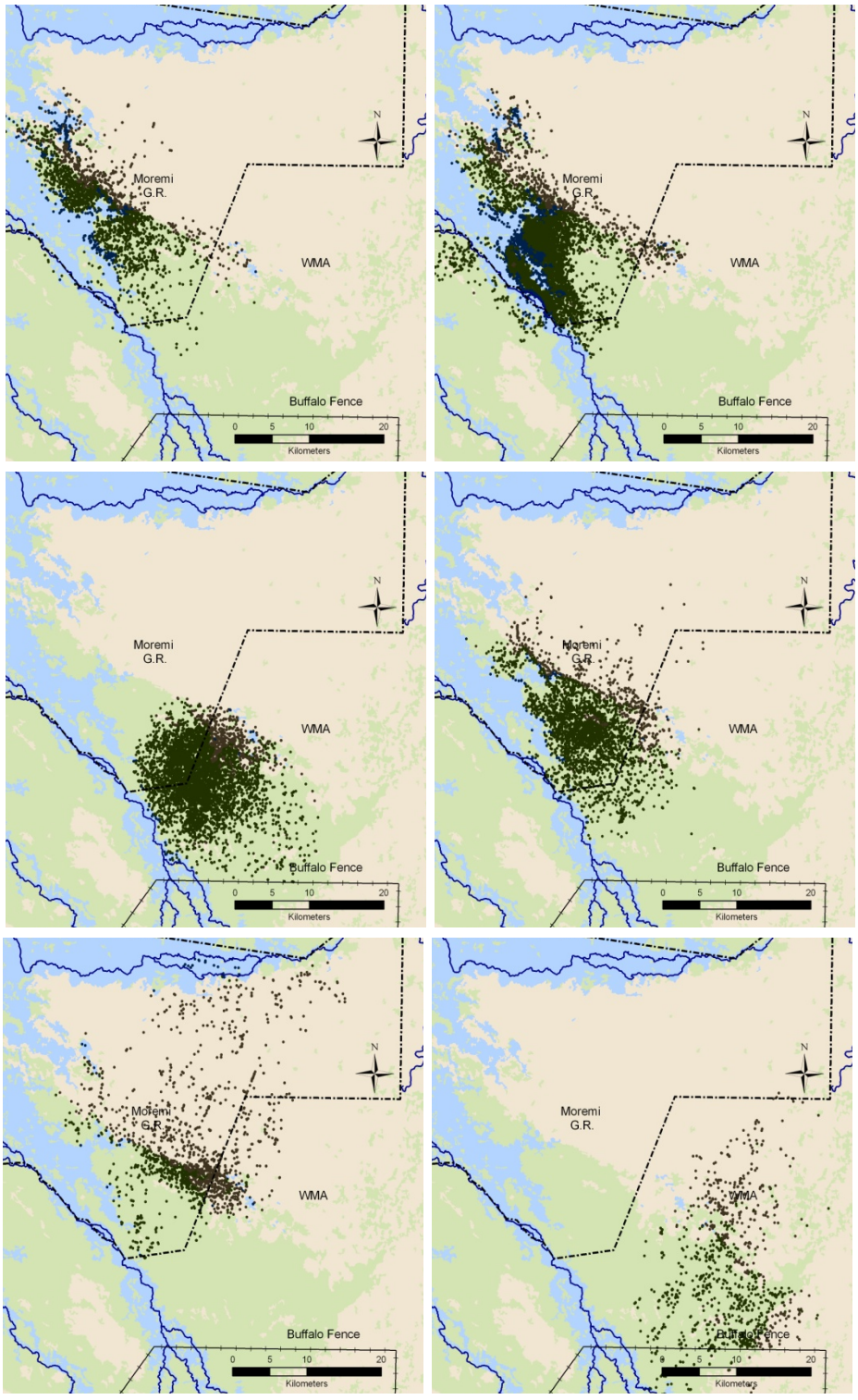


Fig S3: Maps showing the geographical distribution of six individual lions fitted with GPS radio-collars. Each dot represents a GPS location. Note the relatively low number of locations in the mopane woodland (brown). Green: mixed sandveld; blue: floodplains.



Chapter Six

General Discussion, Conservation and Management Implications

GENERAL DISCUSSION

Over the last few decades, populations of large carnivores have declined dramatically worldwide (Gittleman et al. 2001). Relatively stable populations mainly persist within ever-shrinking and isolated protected areas. The resulting overcrowding of such protected areas is likely to increase the frequency of both intra- and interspecific interactions that can have negative consequences on subordinate species, and may eventually lead to extinction events. It is the general consensus that, under natural conditions, African wild dogs are heavily negatively influenced by the larger spotted hyenas and lions (e.g. Creel and Creel 1996, Mills and Gorman 1997). The temporal and spatial behavior of the wild dogs have consequently mainly been interpreted as an evolutionary adaptation to reduce encounters with their two stronger competitors, thus enhancing coexistence (Creel and Creel 1996, Hayward and Slotow 2009).

The major aim of my thesis was to investigate patterns of segregation on high-resolution temporal and spatial scales, and to investigate the mechanisms promoting coexistence between the African wild dog, the spotted hyena, and the lion.

The work presented in *Chapter Two* highlighted a degree of temporal overlap considerably higher than previously described. Such overlap was mainly due to the unexpected nocturnal behavior of wild dogs, which appeared to be actively shifting their activity towards the night hours, provided there was sufficient moonlight (Cozzi et al. in press). On one hand, these findings raise some questions concerning the actual role of spotted hyenas and lions in shaping the activity patterns of wild dogs, which have often been simplistically described as being diurnal to evade interactions (Hayward and Slotow 2009). On the other hand, my results highlight how temporal segregation may only play a marginal role in enhancing coexistence between the three species.

Consequently, it can be expected that spatial segregation represents a key mechanism promoting the coexistence among the three species. In fact, the data presented in *Chapter Three* showed a lion density threshold, above which wild dogs tended to be excluded from particular areas, and both *Chapter Three* and *Chapter Four* suggests that wild dogs may take advantage of areas characterized by a low lion presence (Cozzi et al. in press). This may particularly be the case for critical activities such as the raising of the offspring. An additional important element clearly emerges from both chapters; namely that spotted hyenas do not negatively affect the spatial distribution of wild dogs. My findings are in line with past studies conducted in other ecosystems and support i) the accepted knowledge that lions exert a negative pressure on wild dogs (e.g. Creel and Creel 1998, Mills and Gorman 1998, Webster et al. 2012), and ii) they reinforce the growing evidence that spotted hyenas only marginally negatively influence wild dogs (e.g. Webster et al. 2010, 2012)

It is here, however, indispensable to mention that the likelihood of interactions, both on a temporal and spatial scale, will highly depend on the absolute densities of the interacting species. Therefore, to contextualize our results and allow comparison across different ecosystems, the densities of spotted hyenas and lions were investigated and the results are presented in *Chapter Five*. For the study area, the density of spotted hyenas and lions were estimated to be, respectively, 15.4 adult hyenas /100 km^2 and 16.2 lions /100 km^2. Despite the densities varies among habitat types (particularly the case for lions), these figures compare well with other highly productive ecosystems such as the Kruger National Park in South Africa or large protected areas in eastern Africa that support high numbers of both species (Ogutu and Dublin 1998, Mills et al. 2001). On the other hand, though, our estimates are considerably higher than the densities recorded in drier and less productive ecosystems (for an overview see Bauer and Merwe 2004). The hyena and lion density in the Okavango Delta should therefore be considered to be between medium and high.

It consequently appears that the low degree of temporal segregation observed in the study area cannot be credited to a low density of spotted hyenas and lions resulting in a low likelihood of interactions. I alternatively hypothesize that intrinsic factors and bottom-up forces, such as the activity pattern of prey species, might drive patterns of diel activity in wild dogs (see below). It can, however, be anticipated that above a certain density threshold wild dogs may seek a higher degree of temporal segregation than observed in the study area. I therefore suggest that similar studies be performed in other ecosystem characterized by similar conditions (e.g. vegetation structure and prey base) but different densities of hyenas and lions. Rasmussen and Macdonald (2012), for example, also described a certain degree of nocturnal activity for wild dogs living outside protected areas in absence of lions, and alternatively concluded that the observed activity patterns and behavioral plasticity were a response to human activity. I however clearly showed that wild dogs are active at night even in presences of lions and total absence of humans.

Past studies have shown a negative correlation between the density and distribution of wild dogs and those of spotted hyenas and lions (Creel and Creel 1996, Mills and Gorman 1997, Creel and Creel 2002). However, these relations were investigated on a broad spatial scale and using indirect methods to create utilization distribution maps (so-called landscapes of fear) for spotted hyenas and lions (see for example Creel and Creel 1996). By simultaneously fitting individuals of the three species with GPS radio-collars I was able to create highly precise utilization distribution maps and analyze spatial segregation on a small-scale, within-territory level.

My findings, which apply on a *within-territory* scale, reinforce and expand on the findings by Cree and Creel (2002), who showed a negative correlation between wild dog density and lion density across ecosystems. The data presented in *Chapter Three* suggest that in areas characterized by a low lion presence, wild dogs may take advantage of the

best resources, but that they are restricted in their behavior or even excluded from particular areas above a certain lion density, irrespective of other variable such as habitat type and prey availability. Habitat structure (e.g. visibility) may, however, further influence spatial distribution and interactions among species and I suggest further investigation of the topic, expanding on my findings from *Chapter Three*. Indeed, I measured visibility, but due to inconsistencies in the visibility within and between habitats I could not use this information for the analyses. A more effective approach may be to create habitat visibility maps based on tree densities and possibly correct for such maps using information on grass height. Nevertheless, our result supports the conclusion by Creel and Creel (1996), who stated that conservation of wild dogs might be best achieved in areas with a relatively low presence of lions. On the base of my findings, I see in the large territories of wild dogs the necessity to have areas with differential levels of risk where to retreat when necessary (e.g. when raising the offspring). To evade negative interactions wild dogs may move out from protected areas (where lions densities are commonly high) and into human-dominated landscapes where they suffer direct persecution by humans (van der Meer et al. 2011). Such behavior may work as an ecological trap and negatively influence populations inside protected areas, too (Balme et al. 2009, Balme et al. 2010). Lions may thus be responsible for the fugitive nature of wild dogs (sensu Creel and Creel 1996, Webster et al. 2010, 2012). The negative effect of lions on various aspects of wild dogs behavior and ecology finds general consensus in the literature, and my findings on spatial behavior further support this knowledge.

On the other hand, the role that hyenas play in shaping the spatial-temporal behavior of wild dogs seems to be less unidirectional and I could even find a positive correlation between the spatial distributions of the two species. In areas of high hyena density and good visibility, hyenas quickly aggregate at wild dog kills and reduce their food intake through kleptoparasitism (Kruuk 1972, Fanshawe and Fitzgibbon 1993, Carbone et al.

2005). The loss of prey to hyenas has been pointed out as a possible cause for the observed low populations of wild dogs in regions where the risk of kleptoparasitism is high (Gorman et al. 1998). In more vegetated areas were visual detection of carcasses is reduced, kleptoparasitism events are less frequent and wild dogs enjoy a relatively long access time at a carcass before kleptoparasitizing hyenas may gather at the kill site (Mills and Gorman 1997, Creel and Creel 2002, but see van der Meer et al. 2011). In such areas, hyena likely do not influence wild dogs as negatively as in the open plains of the Serengeti in Tanzania where kleptoparasitism rate can locally be as high as 85.5 % (Fanshawe and Fitzgibbon 1993). As already mentioned above, this shows the importance that habitat structure has in influencing spatial interactions among species. In the study area hyena were present at only about 10% of the wild dog kills (unpublished data) and in most cases only approached when the majority of the prey was already consumed. Under these circumstances it is not surprising that wild dogs did not actively avoid those areas characterized by a high likelihood of encountering hyenas.

Encounters with lions are potentially more detrimental to wild dogs than encounters with hyenas. Lions negatively influence wild dogs mainly through direct predation, accounting for up to 50% of the causes of natural mortality, while spotted hyenas mainly interact with wild dogs through kleptoparasitism (which, as mentioned above, is relatively low in the study area) (Woodroffe et al. 1997). Therefore, considering such costs, it is not surprising that wild dogs tend to consistently avoid areas with a high lion density, while being less affected by the distribution of spotted hyenas. Our findings are in line with findings for the study area by Webster et al. (2010, 2012) who, by means of playback experiments, showed that wild dogs reacted more to lions than to spotted hyenas. Because within large ecosystems, the broad scale distribution and abundance of lions and hyenas are generally positively correlated (e.g. Creel and Creel 1996) it was so far difficult to differentiate to

what extent spotted hyenas and lions, respectively, were responsible for the observed distribution of wild dogs. The small-scale analysis presented in *Chapter Three*, however, suggests that lions and not hyenas mainly inhibit wild dogs.

The observed patterns of spatial segregation suggest that wild dogs have the ability to objectively assess, and possibly predict, the real distribution of risks, and accordingly adjust the use of their territory to minimize such risks. It remains to be understood which cues wild dogs use to discriminate between areas with a high and a low likelihood of encountering lions and I encourage further research on this topic. Such cues may be olfactory, auditory, visual or related to memories of past experiences and possibly based on a medium- to long-term memory. A central question that will need to be asked is for how long these memories and the knowledge of the territory lasts following changes in the distribution of risks (say, following the sudden death of the members of a pride of lions).

Several other factors and life history traits not considered in this study, such as dietary segregation, prey exploitation, hunting success, reproductive rate and success, are likely to contribute to and facilitate coexistence (e.g. Krebs and Davies 1997). I will here very briefly mention some of them. Wild dogs are characterized by a disproportionally large litter size and high reproductive rate and each year, the dominant female gives birth to an average of 10-11 pups (up to a maximum of 16!) in her pack (McNutt and Boggs 1996). These numbers are in clear contrast with the much slower reproductive rate of lions and hyenas that only give birth to 1-4 cubs every two to three years, or 1-2 cubs every two to four years, respectively, depending on the hierarchical status (Kruuk 1972, Schaller 1972, Packer et al. 1990, Smith et al. 2008). Despite more than 50% of the wild dog pups die within the first year of life, this high reproductive rate may put wild dogs at an initial

demographic advantage that enables them to yearly 'replace' individual losses and thus to coexist with the competitively stronger spotted hyenas and lions.

It has also been suggested that subordinate species can coexist with more dominant species provided they are more successful at securing resources (Polis and Holt 1992, Revilla 2002). Wild dogs are extremely skilled hunters and their hunting success has been reported to be 70%, as opposed to spotted hyenas and lions that have a hunting success of about 30–35% (Mills 1990, Holekamp et al. 1997, Funston et al. 2001, Creel and Creel 2002). Even in this case, wild dogs seems to be at an advantage over their direct competitors. The dogs' feeding strategy and ability to gobble several kg of meet within a few minutes further enables them to finish a prey the size of a medium-sized antelope in 30-40 minutes (pers. obs.), thus drastically diminishing losses to direct dietary competition (i.e. kleptoparasitism).

Because predators are tightly coupled with their prey, a complete understanding of the behavior and ecology of impala, which in the study area represent over 90% of the prey of wild dogs (McNutt and Boggs 1996, G. Cozzi data not shown), will be key for the interpretation of some of the observed patterns for African wild dogs. From the data presented in *Chapter Three* and *Chapter Four* it appears that the spatial distribution of wild dogs is not directly positively linked to and influenced by prey distribution. Our results strengthen findings by Mills and Gorman (1997), who reported that wild dog distribution was not positively correlated with impala distribution. The authors suggested that lion avoidance was causing wild dogs to avoid areas with high prey densities.

As mentioned above, prey species may, however, be at the basis of the observed activity pattern of wild dogs. In the literature I could not find any detailed study on impala night activity patterns, but there is some evidence that the species may be actively foraging at night under bright moonlight conditions (Jarman and Jarman 1973). An increased impala

activity during moonlight likely increases their detectability by the cursorial hunting wild dogs, which can then take advantage of the comparatively well-lit conditions to unnoticed get closer to the prey. An increased hunting success at night possibly influences the nocturnal activity pattern of wild dogs. A comprehensive investigation of impala activity patterns could easily be achieved by fitting radio-collars provided with activity sensors, similar to the collars applied to the carnivore species in my studies. This would allow for a better understanding of the forces (top-down and bottom-up) shaping the diel activity patterns of African wild dogs. Such a study could and should be expanded further to analyze the influence of habitat characteristics.

CONSERVATION AND MANAGEMENT IMPLICATIONS

Large carnivores that range over large territories, such as wild dogs, spotted hyenas and lions, inevitably enter in contact with humans and human activities. Such activities will predictably change the animals' behavior, thus influencing coexistence (Woodroffe et al. 2005). In *Chapter Four* I investigated the effects that human activities at the boundary of a protected area can have on the spatial distribution and overlap of large carnivores, and discuss the effects of such activities on the community structure of large carnivores. By excluding some species but not others from particular areas, human activities may ultimately change interactions among animals (Cozzi et al. in press). This could further trigger the succession of a series of cascading events that could ultimately influence the whole community assembly (Lagendijk et al. 2011, Slotow 2012).

A deep understanding of the ecological and anthropogenic factors that form the basis of coexistence between species is essential for their effective management and the creation and implementation of protected areas. Mainly due to direct persecution, in the short to medium term, efforts to ensure the survival of large carnivore species may need to be prioritized in and around such protected areas. Careful management planning should

take into consideration not only large-scale processes, but also information relevant to small-scale events. On one hand, conservation of subordinate species may be best achieved in areas characterized by an overall low density of more dominant species (Creel and Creel 1996). On the other hand, as shown in my study, species may be able to take advantage of small-scale changes in the distribution of their stronger competitors. In my case, wild dogs in the Okavango Delta successfully coexist alongside the more aggressive competitors by exploiting those habitat types less frequented by lions (e.g. mopane woodland) and by shaping their territory and adjusting its use according to alteration in the likelihood of encountering lions. It thus appears that coexistence between wild dogs and lion is possible even in those areas with an overall high lion density (the Okavango), as long as habitat heterogeneity provides small-scale refuges for wild dogs. Competition and predation pressure can furthermore be reduced through enhanced connectivity allowing animal movements between protected areas. This would facilitate free movements of animals from over-crowded reserves into areas where density-dependent conditions for survival are more favorable.

In the long term, however, as a result of an improvement strategy to reduce human-wildlife conflict on one side, and the change in pastoralism and farming practices on the other side, with the progressive abandonment of rural areas, coexistence between predators and humans may be possible. This is for example what is happening in Europe, where ongoing abandonment of agricultural practices and the natural reforestation of large patches of land have permitted wolves and bears to slowly recolonize those areas from which they went extinct due to direct persecution (e.g. Valière et al. 2003).

CONCLUSIONS

This work highlights the need for a multi-species approach, where the effects of top-down and bottom-up forces, as well as human activities, on ecological processes are analyzed

simultaneously. Spatial segregation, rather than temporal segregation, appears to be a key component for the coexistence of African wild dogs, spotted hyenas and lions living under natural conditions. In particular, I show that the spatial distribution of wild dogs is negatively correlated with the distribution of lions, while spotted hyenas do not negatively affect the dogs' spatial behavior. In this context, habitat heterogeneity likely plays a major role in promoting coexistence. The spatial distribution and interactions among the three species is furthermore influenced by human-induced modification of the landscape through exclusion of lions but not of the other species from certain areas. Considering the dramatic rate at which habitat modification, loss and fragmentation are happening, the need to conserve spaces that are large enough to allow species coexistence should sound like a warning bell. Animals are increasingly forced to live within smaller protected areas and the result of this, including overcrowding and negative interactions such as predation and competition, could have negative consequences for subdominant species.

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